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Species interactions in ephemeral patch systems: spatial, temporal, and spatio-temporal influences

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Species interactions in ephemeral patch systems: Spatial,
temporal, and spatio-temporal influences

by

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A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

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For Catherine

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CHAPTER I. INTRODUCTION

Ephemeral patch communities

Many ecological communities are characterized by ephemeral interactions between species associated with discrete patches of biological resources. These patches typically consist of organic matter produced by a single individual of one species that is quickly depleted by multiple individuals of other species, which feed off of the organic matter during development. This ephemerally produced organic matter may be dead tissue such as dung or carrion. In such systems, direct interactions are almost certainly restricted to species using the resource and not the species producing it. In contrast, some patchy resources are produced by the ephemerally available living tissues of organisms, such as the fruits of plants or the fruiting bodies of fungi. For these systems, not only will the availability of patch resources have a direct impact on the species using these resources, but these species may have a direct impact on their hosts in turn through the consumption of living tissue. In all such systems, the turnover of resources within patches is very rapid, occurring over periods of hours or days (Beaver, 1977). Species that use these resources in development typically only produce a single generation before patches become unusable, so they must regularly disperse to new patches to complete their life cycles. Despite this constraint, ephemeral resource patches often support an unusually high diversity of interacting species (e.g., Atkinson and Shorrocks, 1981; Hartley and Shorrocks, 2002). This unusual diversity of species has led to many theoretical and empirical studies that focus on the interactions between species in ephemeral patches, and how these interactions lead to species coexistence (e.g., Shorrocks et al., 1979; Atkinson

and Shorrocks, 1981; Chesson, 2000; Woodcock et al., 2002).

Coexistence of myriad species in ephemeral patch systems is likely facilitated by the spatial, temporal, and spatio-temporal dynamics of species interactions. Species interactions can vary spatially due to environmental heterogeneity, leading to unique ecological and evolutionary outcomes in different locations (e.g., Thompson, 2005, 1994; Thompson and Cunningham, 2002). They can also vary temporally when the environment changes over time (e.g., Descamps-Julien and Gonzalez, 2005; Jiang and Morin, 2007). Finally, the dynamics of species interactions can vary spatio-temporally when spatial locations vary in their temporal dynamics independently (Chesson, 1985), i.e., when the temporal processes in local environments change in a way that is independent of permanent spatial heterogeneities and global environmental changes over time. For many types of interactions, theory suggests coexistence is promoted by spatial (e.g., Amarasekare, 2003, 2004), temporal (e.g., Chesson and Warner, 1981; Chesson and Huntly, 1997; Szilágyi and Meszéna, 2010; Gravel et al., 2011), and spatio-temporal environmental variation (e.g., Comins and Noble, 1985; Taylor, 1998). And given their rapid turnover of resources, and the need for many species to disperse in every generation, ephemeral patch systems are good models for studying how this variation affects species interactions and coexistence.

Plants and their seed-eating pollinators

Plants that are associated with seed-eating pollinators are especially interesting ephemeral patch systems. In these interactions, plants produce ephemerally available flowers that are pollinated by insects. Pollinators lay eggs into a subset of flowers, and these eggs feed on plant seeds during larval development. Although this interaction is often assumed to be inherently mutualistic, it can become commensal or antagonistic in the presence of co-pollinators (e.g., Thompson and Cunningham, 2002). Beyond the defining plant-pollinator interaction, these communities also typically include other types of species interactions at multiple trophic levels. Less often recognized, but nearly as widespread,

are the antagonistic interactions between mutualists and exploiters of mutualisms (Bronstein, 2001*a*). Like pollinators, exploiters feed on the developing seeds of plants, receiving the resource benefits associated with the mutualism without paying the service cost of pollination. As such, the interaction between exploiters and plants is assumed to be parasitic in nature, and the interaction between exploiters and pollinators is characterized by direct competition for developing seeds. In turn, both pollinators and exploiters may be parasitized by additional species of parasitoids, which consume their hosts in development.

In addition to having a diversity of species interactions, plant and seed-eating pollinator communities are especially good models because of the clearly measurable fitness costs and benefits associated with each species. Plant fitness can be both theoretically modeled and empirically measured in terms of seed production, and in the production of pollinators that increase plants' male fitness. The fitnesses of pollinators and associated exploiters and parasitoids can be modeled and empirically measured in terms of developing offspring. Empirical estimates of seed and offspring counts are often easily obtained from dissected plant tissue (Bronstein, 2001*b*), and variation in these estimates can be compared in a straightforward way across multiple systems of plants with seed-eating pollinators. Such systems include the interactions between senita cacti and their pollinating moths (e.g., Holland and Fleming, 1999), and those between globe-flowers and their pollinating flies (e.g., Després and Jaeger, 1999; Després et al., 2007). But most well-studied are those between yuccas and their pollinating moths (e.g., Keeley et al., 1984; Addicott, 1986; Keeley et al., 1986; Pellmyr and Huth, 1994) and figs and their pollinating wasps (e.g., Janzen, 1979; Bronstein, 1988; Herre and West, 1997; Weiblen, 2002).

Figs and their pollinating and non-pollinating wasps

The interaction between figs (*Ficus*, Moraceae) and their pollinating wasps (multiple genera, Agaonidae) is a classic plant and seed-eating pollinator mutualism. All 750+ species of figs produce enclosed inflorescences, typically referred to as fruit but technically syconia, which hold tens to thousands of uni-ovulate female florets. Production of syconia within the crown of individual fig trees is never continuous, and is often synchronous with bouts of reproduction separated by many months and even a few years (Bronstein, 1989; Windsor et al., 1989). To maintain viable fig and wasp populations, pollinators must regularly move to new fig trees with receptive syconia, routinely dispersing distances of tens of meters to tens of kilometers (Nason et al., 1996, 1998; Ahmed et al., 2009). Mated, pollen-bearing, adult female wasps (foundresses) are attracted to fig syconia when receptive flowers produce wasp-species-specific volatile chemicals. Foundresses enter syconia through a small bract-lined opening (the ostiole), then actively or passively pollinate female flowers while laying eggs into a subset of ovules before dying within syconia (Janzen, 1979). Wasp larvae develop for several weeks before wingless males emerge and compete for access to females (often full siblings). After mating, females collect pollen and exit syconia through holes chewed out by male wasps.

Like most mutualisms (Bronstein, 2001*a*), the fig-fig wasp mutualism is exploited by species that receive mutualism resources without providing goods or services in return. These exploiters make up much of the diverse communities of non-pollinating fig wasps, galling fig flowers like pollinators without providing pollination services to the fig. Some non-pollinators, in contrast, make use of other resources within the syconia. These non-pollinators include wasps that oviposit early in syconia development and induce especially large galls from the syconia wall (Kerdelhué et al., 2000). Others are inquilines, which kill pollinators and feed on developing seed tissue (Dunn et al., 2008). Additionally, parasitoid fig wasps may attack other species of pollinating and non-pollinating fig wasps,

consuming the offspring of their hosts in larval development. As with pollinators, non-pollinators are usually host-fig-specific (Weiblen, 2002), and a single species of fig can host between 3 and 30 non-pollinator species (Compton and Hawkins, 1992).

The fig wasp community surrounding the Sonoran Desert rock fig (*F. petiolaris*) includes a diverse but tractable assemblage of species, which makes it especially amenable to studies of interspecific interactions. A member of pan-tropical subgenus *Urostigma*, *F. petiolaris* is in the section *Americana*, and occurs in Baja California, and parts of mainland Sonora, Mexico. It is obligately associated with a pollinating and seed-eating wasp in the genus *Pegoscapus* (un-named species; Family Agaonidae). In addition to the pollinator, seven non-pollinating species of wasps oviposit into *F. petiolaris* syconia. In contrast to the pollinator, these non-pollinator species oviposit from outside syconia, inserting their ovipositors through syconia walls. The non-pollinating wasps of *F. petiolaris* include four genera, three species of which belong to *Idarnes* (Subfamily Sycophaginae with taxonomic affinities unclear; Rasplus and Kerdelhué, 1998), which is the most abundant genus of non-pollinating fig-wasps in the Americas (Bronstein, 1991; West and Herre, 1994; West et al., 1996). Also found in the *F. petiolaris* wasp community are two species of *Heterandrium* (Subfamily Otitsellinae, Family Pteromalidae). All species of *Idarnes* and *Heterandrium* oviposit into fig flowers and produce larvae that each develop at the cost of a single developing seed. *F. petiolaris* is additionally associated with wasps of the genus *Aepocerus* (Subfamily Otitsellinae, Family Pteromalidae), which appear to gall tissue that originates from the syconia wall. *Aepocerus* wasps are parasitized by wasps of the genus *Physothorax* (Family Torymidae).

Dissertation objectives

The objectives of this dissertation are to develop and test hypotheses related to the influence of spatial, temporal, and spatio-temporal processes on species interactions in ephemeral patch communities. These objectives are accomplished using a combination

of theory and observational hypothesis testing. Theory is developed using numerical and individual-based models combined with computationally intense simulations. Specific hypotheses obtained from models are tested using empirical data collected from the fig-wasp community surrounding *F. petiolaris*. Conceptually, because ephemeral patch communities are characterized by regular dispersal among patches in space, and rapid turnover of patch resources in time, spatial, temporal, and spatio-temporal processes in these communities are expected to be especially influential for species interactions. Specifically, this dissertation models the impact of plant habitat heterogeneity and autocorrelation on the interactions between a plant, its mutualist pollinator, and an exploiter of the mutualism. The ecological patterns predicted from this model are tested using geographic and abundance data from *F. petiolaris*, its pollinator, and associated non-pollinators. This dissertation also models how the ephemeral availability of patch resources affects specialist competitors that use these resources in development – particularly their life histories and coexistence. The life history traits predicted from this model are tested using five non-pollinating galler wasps specific to *F. petiolaris*, which compete for access to fig flowers.

Dissertation organization

In Chapter II, Matthew Falcy and I develop an individual-based, spatially explicit, model to examine the impact of plant habitat heterogeneity and autocorrelation on the interactions between a plant, its obligate seed-eating mutualist pollinator, and an obligate seed-eating exploiter of the mutualism when individual dispersal is limited. We test how habitat autocorrelation affects key properties of the plant-pollinator interaction, including pollinator production, seed production, pollinator visitation to plants, and the coexistence of plants, pollinators, and exploiters. The modeling work we develop builds on the modeling work of Wilson et al. (2003), Morris et al. (2003), and Bronstein et al. (2003). The ecological patterns and spatial mechanisms observed from this chapter are

used to develop empirical hypotheses that are tested in Chapter III.

Using the modeling from Chapter II, John Nason and I test four hypotheses specific to the plant-pollinator-exploiter community surrounding *F. petiolaris*. We use geographic coordinates of trees from six *F. petiolaris* populations in Baja California, then test how tree aggregation affects pollinator visitation, seed production, and non-pollinator production using count data from ripe fig syconia. Specifically, we test the following hypotheses: 1) Pollinator visitation to receptive fig trees will increase with tree aggregation, 2) pollinator production will increase with pollinator visitation, 3) seed production will decrease with fig aggregation, and 4) non-pollinator production will decrease with fig aggregation. We discuss how our results contribute to a broader conceptual understanding of spatial dynamics and the ecology and evolution of plant-pollinator communities, and why this understanding may be of importance for conservation.

Chapter IV examines the dynamics of ephemeral patch communities from the perspective of competitors for patch resources. In this chapter, Karen Abbott, John Nason, and I develop a lottery model to examine the impact that the temporal storage of developing competitors has on competitor population dynamics, trait evolution, and coexistence. This chapter adapts the models of Chesson and Warner (1981) and Chesson (1982) to an ephemeral patch community in which within-patch resources are discrete, and tests to what extent temporal variability in the minimum travel distance between patches facilitates competitor coexistence given a life history trade-off between competitor dispersal ability and fecundity. Prior models have shown that a varying environment can lead to long-term competitor coexistence when there is sufficient positive covariance between the effects of environment and competition on competitor growth rate (e.g., Chesson and Warner, 1981; Chesson, 1982; Chesson and Huntly, 1997). Previous theoretical and empirical studies have interpreted environmental effects in terms of physical aspects of the environment such as precipitation (e.g., Pake and Venable, 1995; Angert et al., 2009),

temperature (e.g., Pake and Venable, 1995), germination probability (e.g., Snyder and Chesson, 2004; Snyder and Adler, 2011), or in predation (e.g., Cáceres, 1997). Although very general remarks on variation in patch quality and accessibility have been proposed as important environmental variables (Chesson, 2000), our model is unique in specifically positing that spatial variation in dispersal distance can generate the necessary mechanism for the environmental variation needed to facilitate coexistence. We interpret our model with respect to the diverse assemblages of species-specific non-pollinating fig wasps that compete for access to fig ovules for oviposition sites. The life history trade-off that predicts coexistence in our model is applied to testing hypotheses using the non-pollinating galler community of *F. petiolaris* in Chapter V.

In Chapter V, Karen Abbott, John Nason, and I test the hypothesis that competing non-pollinator fig wasps associated with *F. petiolaris* exhibit a life history trade-off between their fecundities and their abilities to disperse to new receptive fig trees. To test this hypothesis, we dissect females from five species of wasps following the procedure of Ghara and Borges (2010) to estimate wasp fecundity. To estimate dispersal ability, we measure wing loadings for each species, and develop a novel colonization index based on wasp abundances in ripe syconia and syconia volume. We interpret our results in relation to the ideas of Hutchinson (1961), who viewed a stochastically varying environment to play a major role in community diversity.

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CHAPTER II. THE INFLUENCE OF HABITAT AUTOCORRELATION ON PLANTS AND THEIR SEED-EATING POLLINATORS

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Abstract

Model systems for studying mutualism costs and benefits include the many species of plants that rely on seed-eating pollinators for their reproduction. Empirical studies of these interactions show that mutualism costs and benefits can vary greatly within populations. Here we investigate the role of plant habitat autocorrelation on mutualism properties when mutualist dispersal is limited. We build a spatially explicit individual-based model of an obligate mutualism that includes a plant and its obligate seed-eating pollinator. We also model exploiters of this mutualism, which do not pollinate, but compete with pollinators for pollinated plant ovules in which to develop. We test how the autocorrelation of habitable plant environment affects pollinator production, seed production, pollinator visitation to plants, and the persistence of exploiters at different dispersal distances and rates of exploitation. We find that positive habitat autocorrelation increases the mean number of pollinator visits to plants. More frequent pollinator visitation to plants increases the probability that a random plant will be pollinated, but

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also the probability of pollinator oviposition into plant ovules at the cost of a developing seed. This process leads to spatial variation in the production of pollinators versus seeds. For a given scale of habitat autocorrelation, the turnover of this variation decreases when pollinator dispersal distance is high. Exploiters of the mutualism dramatically lower the number of pollinator visits per flower, which decreases pollinator production, seed production, and mutualist densities. Exploiters persist with mutualists when the mean number of pollinator visits per plant is neither too low, nor too high. When the mean number of pollinator visits a plant receives is too low, overexploitation and the extinction of both mutualists and exploiters follows; a high mean number of pollinator visits results in the competitive exclusion of exploiters by pollinators. Because the autocorrelation of habitat strongly affects the number of pollinator visits per flower, our results show that habitat autocorrelation can influence key mutualism properties and the susceptibility of mutualisms to exploitation.

1 Introduction

A mutualism is a type of interspecific interaction in which two or more species exploit one another for mutual gain. Model mutualisms include obligate plant-pollinator interactions in which pollinators consume seeds as a resource during development. Interactions among plants and their seed-eating pollinators are among the most well-studied of mutualisms partly because the costs and benefits associated with these mutualisms can be measured with straightforward estimates of seed and pollinator production (Bronstein, 2001). Such estimates of mutualism properties have been assessed in many empirical systems, including the well-studied interactions between yuccas and their pollinating and seed-eating moths (e.g., Keeley et al., 1984; Addicott, 1986; Keeley et al., 1986), figs and their associated wasps (e.g., Bronstein, 1988; Herre and West, 1997), senita cacti and their moth pollinators (e.g., Holland and Fleming, 1999), and globeflowers and the flies that pollinate them (e.g., Pellmyr, 1989; Després et al., 2007). Bronstein (2001) notes that many studies of these interactions find great variation in fitness costs and benefits at the population level (e.g., Keeley et al., 1984; Addicott, 1986; Keeley et al., 1986; Pellmyr, 1989), and emphasizes the importance of understanding this variation for predicting the strength and nature of plant-pollinator interactions, and the evolution of mutualism properties. Focusing on the Florida Strangling Fig (*Ficus aurea*) and its pollinating wasp (*Pegoscapus mexicanus*), Bronstein (2001) observed variation in fig morphology and the number of pollinators arriving to figs to be driving much variation in mutualism costs and benefits. Here we focus on pollinator dispersal to receptive plants, how the spatial distribution of plant habitat affects pollinator and seed production, the density of plants and pollinators, and the susceptibility of the mutualism to exploitation.

Mutualisms are often associated with one or more exploiter species that use resources from one mutualist without providing anything in return. In model systems of mutualisms with seed-eating pollinators, these exploiters do not pollinate and typically feed off of

developing seeds after pollination occurs. Such exploiters are thus obligately dependent upon both mutualists and compete with pollinators for access to developing plant seeds. The obligate and species-specific nature of this three-way interaction facilitates modeling the community (Wilson et al., 2003). Because many exploiter species in these systems can only oviposit into flowers that have been pollinated, they can directly affect the production of seeds, but not the production of pollinators. In contrast, pollinators can directly affect the production of both seeds and exploiters. To reproduce, pollinators must first disperse to plants with ovulating flowers, and exploiters must disperse to flowers that have ovulated and been pollinated. The movement of both pollinators and exploiters on a landscape is thus expected to strongly influence the population dynamics of these species and the susceptibility of plant-pollinator mutualisms to exploitation.

The effects of dispersal on interspecific interactions can be explored with spatially explicit models. In these models, a spatially explicit, environmentally uniform landscape often facilitates community coexistence and can sometimes reveal interesting spatial dynamics (e.g., Holmes et al., 1994; Wilson et al., 1995, 1993; Wilson and Hassell, 1997). When the assumption of environmental uniformity on a landscape is violated, community dynamics can change dramatically. By adding landscape-level environmental heterogeneity to a host-parasitoid model, Singh et al. (2004) show that even slight deviations from landscape uniformity can break spatio-temporal population synchrony. In mutualistic interactions, landscape heterogeneity has been shown to affect population dynamics and community coexistence, sometimes in counter-intuitive ways. For example, Amarasekare (2004) found that dispersal of mutualists between habitat patches can facilitate coexistence by maintaining sink populations of mutualists, but if dispersal becomes too high between patches, source growth rates can decrease from Allee effects and lead to the regional extinction of both mutualists. The sensitivity to changes in dispersal is even greater for obligate mutualisms (Amarasekare, 2004). Hence, the movement of pollina-

tors on a landscape is likely to influence mutualism properties, including the interactions between plants, pollinators, and their exploiters. The frequency at which mutualists visit plants and exclude exploiters may be affected by demographic properties of individuals, but also by the distribution of habitat on a landscape, which is usually positively spatially autocorrelated (Lennon, 2000). For example, the tropical understory plant *Cordia nodosa* hosts and provides food for ant species, which in turn defend the tree from herbivory (Davidson and McKey, 1993). For ants of the genus *Azteca*, this interaction is mutualistic, but for a species of *Allomerus* ants, which castrate their *C. nodosa* host, the interaction is parasitic. In this system, ants face a trade-off between fecundity and their ability to colonize hosts; foundresses of *Azteca* are better at colonization, but colonies of *Allomerus* are more than twice as fecund (Yu et al., 2001). In locations wherein host plants are more dense, *Allomerus* is relatively more abundant than *Azteca* (Yu et al., 2001). Yu et al. (2001) conclude that both habitat heterogeneity and the spatial arrangement of habitat influences coexistence in these ant-plant systems.

The effects of individual movement have been explored in models of plants, their obligate seed-eating pollinators, and seed-eating exploiters on a uniform landscape of habitat (Bronstein et al., 2003; Wilson et al., 2003). Here we extend the obligate plant-pollinator-exploiter model community of Wilson et al. (2003) with the addition of habitat heterogeneity and habitat arrangement by dividing a landscape into areas in which plants are able to inhabit and areas that they cannot inhabit at varying levels of habitat autocorrelation. Uninhabitable landscape in our model might include areas already inhabited by plants of other species or areas in which the abiotic conditions are too poor to permit plant establishment or flower ovulation. Our model addresses how landscape heterogeneity and autocorrelation affect plant and pollinator density, pollinator production, seed production, and mutualism susceptibility to exploitation.

2 Model

2.1 *The plant-pollinator community*

Like previous models of obligate mutualisms in the presence of obligate exploiters (e.g., Bronstein et al., 2003; Morris et al., 2003; Wilson et al., 2003), we use time increments of a single discrete season over which the interactions between plants, pollinators, and exploiters occur. The modeled order of interactions among plants, pollinators, and exploiters reflects the biological order of their interactions, and the discrete nature of the model is reflected in the seasonality of plant reproduction (Figure 1; Wilson et al., 2003). Our model builds off those of Morris et al. (2003) and Wilson et al. (2003), which describe the change in the density of plants (P), pollinators (M), and exploiters (E) over a season (t). Within a season, a smaller window of time (τ) exists for pollinators and exploiters to visit plants at a rate of η and ε , respectively, before individuals of each species (i) are lost to background mortality with a probability of δ_i . The demographic parameter values we use are identical to those of Wilson et al. (Table 1; 2003).

We use a torus landscape with multiple square cells to construct a spatially explicit individual-based model (IBM) of this community. In our model, individuals occupy a single cell, and cells can be empty or contain individuals of one or more species. Only one plant can occupy a particular cell, but any number of pollinators and exploiters can occupy the same cell. In a single season of the model, each plant on the landscape occupies a single cell and produces one flower that ovulates with a probability of θ .

Pollinators disperse from their natal cell to new cells, some of which contain ovulating flowers. During dispersal, a pollinator moves to a random cell within a Euclidean distance of Δ_M cells in any direction of its previously occupied cell. If the cell at which it arrives is empty, it moves to another random cell within Δ_M cells of the last. If the cell at which it arrives is occupied by a plant with an ovulating flower, it will pollinate the flower and oviposit into the flower with a probability of γ . A pollinated flower is still

a potential resource for pollinator oviposition, but a flower with a developing pollinator cannot become a seed. The dispersal of a pollinator is exhausted when the pollinator has moved $\text{Poisson}(\eta\tau)$ times, which leads to variation in both visitation and dispersal distance per season among individual pollinators. After dispersal, the pollinator will die with a probability of δ_M . Pollinators that do not die remain in the cells they last visited until the following season, when all developing pollinators will mature.

After pollinator dispersal, exploiters disperse from their natal cells to a random cell within a Euclidean distance of Δ_E cells in any direction of their previously occupied cell. If after dispersing an exploiter does not arrive on a plant cell with a flower that has been pollinated, it will move to another cell. If an exploiter arrives on a plant cell with a flower that has been pollinated, but does not already contain a developing pollinator or exploiter, the exploiter will oviposit into the flower. The dispersal of an exploiter is exhausted when the exploiter has moved $\text{Poisson}(\varepsilon\tau)$ times, and the exploiter will die with a probability of δ_E at the end of the season. Like pollinators, exploiters that do not die remain in the cells they last visited. Newly developing exploiters will be mature in the following season.

After pollinators and exploiters have dispersed, flowers that were pollinated but not used for oviposition develop into seeds that disperse to a random cell within Δ_P cells in Euclidean distance of their mother plant. If a seed lands in a cell that is not habitable, or is already occupied by another plant, the seed will die. If the seed lands in a habitable cell that is unoccupied, it will immediately develop into a new plant that can ovulate in the following season. After all seeds have dispersed, new and old plants die with a probability of δ_P .

2.2 *The landscape*

We model the community on a 128×128 torus landscape, which has cyclical boundary conditions whereby opposing edges of the landscape are effectively joined together.

The advantage of this approach is that there are no edge effects because all cells on the landscape are spatially equivalent (Comins et al., 1992). The landscape is divided into cells that are habitable for plants, and cells that plants cannot use. To construct habitable cells that are autocorrelated on the landscape, we generate real values in cells that are spatially autocorrelated using a power spectrum function. This process generates varying levels of autocorrelation using different degrees of stochastic noise, which are often described by the color of their spectra (Lennon, 2000). The spectra have a simple relationship between their density (S) and frequency (f ; Voss, 1988) such that:

$$S_f \propto f^{-\beta} \quad (1)$$

This relationship allows us to vary the level of spatial autocorrelation of values on the landscape with a single parameter (β). We use β values that range from 0 (random habitat placement) to 6 (high habitat autocorrelation; see Figure 2 for examples).

Following Yearsley (2005), to produce a square landscape, we start with a 128×128 matrix (U) in which every column (u) is an identical vector of frequencies. For a 128×128 landscape, values for these frequencies increase linearly from zero to 0.5, then decrease until the last vector element is equal to the second vector element such that $u = [0.0000000, 0.0078125, 0.015625 \dots 0.5000000, 0.4921875, 0.4843750 \dots 0.0078125]$ (see Yearsley, 2005). A matrix of spectrum densities is then generated by

$$S_f = (U^2 + V^2)^{\frac{-\beta}{2}}, \quad (2)$$

wherein V is the transpose of U . Infinite values are set to zero, and a 128×128 matrix (Φ) of random phase shifts (elements are random uniform numbers from zero to one) is generated. To get a matrix of autocorrelated values, we take the real components of an

inverse fast Fourier transformation on M , which is calculated as follows:

$$M = S_f^{\frac{1}{2}} (\cos(2\pi\Phi) + i \sin(2\pi\Phi)). \quad (3)$$

The transformation on M produces a 128×128 matrix of autocorrelated real values, the errors of which are normally distributed. To model a torus landscape with autocorrelated habitat, we select the 30% of cells on the matrix that have the highest values and model them as habitable cells for plants (Figure 2). The remaining cells are modeled as not habitable.

2.3 Verification of IBM accuracy

Wilson et al. (2003) model a single season of plant, pollinator, and exploiter interactions with the following equations:

$$\frac{\Delta P}{\Delta t} = \theta P [1 - e^{-(1-\gamma)\eta\tau M}] (e^{-\gamma\eta\tau M}) (e^{-\varepsilon\tau E}) [1 - (1 - \delta_P \Delta t) P] - \delta_P P \quad (4)$$

$$\frac{\Delta M}{\Delta t} = \theta P [1 - e^{-\gamma\eta\tau M}] - \delta_M M \quad (5)$$

$$\frac{\Delta E}{\Delta t} = \theta P [1 - e^{-(1-\gamma)\eta\tau M}] (e^{-\gamma\eta\tau M}) (1 - e^{-\varepsilon\tau E}) - \delta_E E. \quad (6)$$

To ensure that our IBM was functioning properly, we used the demographic parameter values found in Wilson et al. (Table 1; C code available upon request; 2003), set $\theta = 0.3$, and allowed species in our IBM to disperse without limitation over a homogeneous 128×128 landscape (all cells are habitable). We then compared the population dynamics of our IBM to those of the numerical simulations of equations 4-6. In the absence of dispersal limitations, only stochasticity should engender a difference between the numerical model (Morris et al., 2003) and our IBM. We compared the simulated equations to our IBM with unlimited dispersal at three different exploiter cell inspection rates. At low exploiter

cell inspection ($\varepsilon = 15$), populations are stable. When exploiter cell inspection rate is increased ($\varepsilon = 20$), populations in both the numerical model and the IBM begin to cycle (Wilson et al., 2003); stochastic effects occasionally result in extinction in the IBM when cycling occurs. When exploiter cell inspection rate is high ($\varepsilon = 25$), all three species become extinct. We interpret this as strong evidence that the population dynamics of our IBM accurately reflect those of the equations in Wilson et al. (2003) and Morris et al. (2003).

2.4 *Habitat autocorrelation and mutualism properties*

We test the effect of habitat autocorrelation (β) on properties of the plant-pollinator mutualism at all combinations of short ($\Delta_i = 2$) and long ($\Delta_i = 10$) distance dispersal for each mutualist. We select these distances for short and long dispersal to be identical to those modeled by Wilson et al. (2003). For each combination of mutualist dispersal distances, we run simulations in the absence of exploiters and in the presence of exploiters with simulations of short and long distance exploiter dispersal. We examine values of β ranging from 0 (random habitat placement) to 6 (highly autocorrelated habitat) increasing by increments of 0.5. Other parameters are set to default values (Table 1), and individuals are randomly placed in all simulations with initial population densities of $P = 0.3$, $M = 0.19$, and $E = 0.05$. In a single season, the maximum distance a random short dispersing pollinator moves from its initial location is 3.6 cells, while the maximum distance a random long dispersing pollinator moves is 15.7 cells. For any given habitable cell on the landscape, the density of habitable cells within a 3.6 or 15.7 cell radius increases with β , but this increase is slower and peaks more quickly for the 15.7 cell radius associated with long distance pollinator dispersal (Figure 3). We simulate plants and pollinators on the landscape for 1000 seasons, which allow populations to reach stationarity, before calculating the densities of plants, pollinators, and exploiters. On season 1000, we also calculate mean pollinator and seed production per plant, and

the mean number of pollinator visits plants received. Data collection is repeated for 100 unique landscapes at each level of habitat autocorrelation.

2.5 Habitat autocorrelation and community coexistence

To estimate the effect of habitat autocorrelation on community coexistence and the spatial dynamics of interacting species, we simulate different habitat autocorrelations (β), dispersal values (Δ_i), and exploiter cell inspection rates (ε). Like tests of mutualism properties, we use values of β ranging from 0 to 6 by increments of 0.5 at different combinations of short and long distance dispersal in different species, and we examine three levels of exploiter cell inspection rate. These three levels include low ($\varepsilon = 15$), medium ($\varepsilon = 20$), and high ($\varepsilon = 25$) cell inspection rate as used in Wilson et al. (2003). Other parameters are set to default values (Table 1). To test for community coexistence at different parameter combinations, individuals are randomly placed on the landscape at starting densities of $P = 0.3$, $M = 0.19$, and $E = 0.05$; coexistence results were found to be robust to different starting densities. One thousand seasons are run for each simulation, and extinction events are recorded in each of 100 simulations for each parameter combination. For each parameter combination, we also record the spatial and spatio-temporal dynamics of individuals. To examine the spatial distributions of plants, pollinators, and exploiters, the positions of individuals are recorded after 500 seasons of a simulation. We examine the spatio-temporal dynamics of individuals with the space-time (XT) images used in Bronstein et al. (2003) and Wilson et al. (2003); we sample a single transect row from the 128×128 landscape at every season (Supplemental Material S1).

2.6 Model sensitivity to θ , γ , and η

To determine how the results of our model depend on the seasonal probability of flower ovulation (θ), the probability that a pollinator oviposits after pollinating (γ), and pollinator cell inspection rate (η), we vary each of these parameters to assess how variation

in θ (0.7-1.0), γ (0.3-0.7), and η (4-8) affect species densities, pollinator production, seed production, pollinator visits received by plants, and community coexistence. In all of these simulations, parameters not varied are set to their default values (Table 1), and all species have short distance dispersal.

3 Results

The 100 replicate simulations resulted in means with very low standard errors for all parameter combinations used. Error bars showing a 95% range around each point would not be clearly distinguishable from the points in the figures, so we omit them in presenting our results. An example of the consistency of these results for the mean number of pollinator visits per flower can be found in the Supplemental Material (S2).

3.1 *Habitat autocorrelation, species densities, and mutualism properties*

All simulations of plant-pollinator interactions in the absence of exploiters resulted in long-term coexistence of mutualists. In the absence of exploiters, the relationship between habitat autocorrelation and the density of plants and pollinators differed depending on the dispersal abilities of the mutualists. For all combinations of long and short mutualist dispersal, the increase in habitat autocorrelation led to an increase in the mean number of times that a random plant was visited by a pollinator in a season (Figure 4c). This increase in pollinator visits per flower was caused by the aggregation of pollinators in areas of the landscape containing habitable cells for plants. When these habitable cells were autocorrelated, plant distribution was likewise autocorrelated. Pollinators, which initially emerge from plants used for oviposition, have a higher likelihood of visiting cells in the vicinity of their natal plant – especially if these pollinators disperse short distances. If the spatial distribution of plants is autocorrelated, nearby cells are more likely to be habitable and contain plants, so the number of pollinator visits per flower increases with increasing habitat autocorrelation, most dramatically when pollinators have short distance dispersal

(Figure 4c). The increase in pollinator visits per flower reduces the probability that a plant goes unpollinated, but it also increases the probability of pollinator oviposition due to the likelihood of repeated pollinator visits. And in the absence of exploiters, mean pollinator production per plant increased (Figure 4b), and mean seed production per plant decreased (Figure 4a), as habitat became more autocorrelated. This increase in pollinator production and decrease in seed production was strongest at low pollinator dispersal, leading to a decrease in plant density (and, in turn, pollinator density) at higher levels of habitat autocorrelation (Figure 5a) as plants became less likely to produce seeds. The mean number of visits pollinators made to plants at high habitat autocorrelation was lower when pollinators had long distance dispersal, and plant density did not decrease at higher levels of habitat autocorrelation as a result of increased pollinator oviposition probability, which was balanced by the decreased likelihood of plants going unpollinated.

When exploiters of the mutualism were included in simulations of plant-pollinator interactions and able to avoid extinction for 1000 seasons, mutualist density, seed production, pollinator production, and the mean number of pollinator visits per flower declined at all levels of habitat autocorrelation. The nature of the effect of exploiters on these species densities and mutualism properties was not different for short versus long distance exploiter dispersal, but long dispersing exploiters were more likely to go extinct than short dispersing exploiters because short dispersing exploiters were more likely to search cells near their natal plant; when habitat was autocorrelated, these nearby cells were more likely than distant cells to be receptive to exploitation. For simplicity, we focus on the effects of exploiters only when dispersal is short. In these simulations, the extinction of exploiters occurred only when pollinator dispersal was short and the level of autocorrelation was higher than $\beta = 2$. When exploiter extinction occurred, plant and pollinator densities after 1000 seasons in these simulations were generally the same as in simulations without the inclusion of exploiters (Figure 5a,b), as was seed production,

pollinator production, and flower visitation rate (Figure 4). When exploiters persisted, plant density was only ca 1/2 of what it was in the absence of exploiters, and the density of pollinators dropped to ca 1/5 of its density in exploiters' absence; this was consistent across all levels of habitat autocorrelation (Figure 5). Because exploiters oviposit after pollinators in each season, exploiters can only directly affect the production of seeds by using flowers that have been pollinated, but not used by pollinators for oviposition. As such, the decrease in seed production caused by exploiters led to a subsequent decrease in plant density. When plant density was reduced by exploiters, fewer pollinators were produced, and the mean number of pollinator visits per flower dropped dramatically (Figure 4c). For example, in the absence of exploiters, when plant seeds had short distance dispersal and pollinators long distance dispersal, the mean number of pollinator visits per flower rose from a mean of 3.1 pollinators per season at the lowest level of habitat autocorrelation (more randomly scattered habitat) to 5.5 pollinators per season at the highest level of habitat autocorrelation. But when exploiters were included in these simulations, the mean number of pollinator visits per flower ranged only between 0.74 and 1.2 pollinators per season.

3.2 *Habitat autocorrelation and community coexistence*

We recorded the proportion of long term coexistence of plants, pollinators, and exploiters using the same dispersal combinations as in Wilson et al. (2003) for multiple levels of exploiter cell inspection rate. Long term coexistence of mutualists and exploiters was greatly affected by the level of habitat autocorrelation (β) at different relative species dispersals (Δ_i) and exploiter cell inspection rates (ε ; Figure 6). In all simulations, as expected (Wilson et al., 2003), exploiters were the first species to become extinct when extinction occurred. Sometimes this extinction occurred because exploiters were competitively excluded by pollinators. This happened at higher β values in which pollinators were more aggregated (Supplementary Material S1) and the mean number of pollinator

visits per flower was higher (Figure 4c) resulting in higher pollinator oviposition per plant (Figure 7). When the probability of pollinator oviposition increased, fewer pollinated flowers were available for exploiters to use (Figure 7c). The mean number of pollinator visits per flower was also affected by the dispersal distance of pollinators; long distance dispersal lowered the number of flower visits, and subsequently pollination, when habitat was autocorrelated because pollinators were less likely to visit nearby cells on the landscape. This resulted in the persistence of exploiters at higher values of β when pollinators dispersed longer distances (Figure 5c). As expected, increasing ε lowered the probability of exploiters being competitively excluded by pollinators; when exploiters were able to visit more cells in a season, pollinated plants available for exploiter oviposition were more likely to be used.

In some simulations, the extinction of exploiters was quickly followed by the extinction of both mutualists (Figure 6). The extinction of the entire community occurred when the mean number of pollinator visits per flower was low, and exploiter cell inspection rates were high. Fewer pollinator visits to flowers decreased the probability of plants experiencing pollinator oviposition, increasing the proportion of pollinated plants available to exploiters. When exploiter cell inspection rates were high enough to take advantage of the high proportion of available pollinated flowers in these communities, seed production was also lowered, and the densities of both mutualists and exploiters fell until all three species became extinct.

3.3 Sensitivity to θ , γ , and η

Decreasing the probability of plant ovulation (θ) did not affect the mean number of seeds a plant produced (Figure 8a) and consistently decreased the mean number of pollinators produced (Figure 8d) and pollinator visits per plant (Figure 8g). At all values of θ , seed production decreased with increasing habitat autocorrelation, and pollinator production and pollinator visits per flower increased with habitat autocorrelation.

Exploiters were always competitively excluded by pollinators when $\beta \geq 2$.

Increasing the probability of pollinator oviposition (γ) decreased seed production (Figure 8b), especially at low habitat autocorrelation, in which the mean number of pollinator visits a flower received was low (Figure 8h). The increase in seed production that resulted from more pollinator visits without oviposition at low γ values was less dramatic at high habitat autocorrelation in which pollinator visits were more frequent; pollinator production increased slightly with increasing β (Figure 8e), and was affected little by differences in γ . Interestingly, low pollinator oviposition ultimately resulted in higher pollinator densities – the increase in seed production at lower pollinator oviposition led to a higher density of plants for pollinators to use as a resource for oviposition. Low pollinator oviposition also made exploiter persistence more likely, and resulted in exploiters driving all three species to extinction at low levels of pollinator oviposition and habitat autocorrelation.

Increasing the number of cells pollinators were able to visit in a season led to a predictable decrease in seed production (Figure 8c) as the mean number of times a plant was visited by a pollinator increased (Figure 8i). Plant visitation by pollinators increased with increasing habitat autocorrelation, which resulted in lower seed production and higher pollinator production as β increased. Competitive exclusion of exploiters by pollinators occurred at all but the lowest value of $\eta = 4$ in which coexistence was possible when $\beta < 3$. When $\eta = 4$ and $\beta = 0$, exploitation led to the extinction of all three species.

4 Discussion

Positive autocorrelation is observed in most spatial data in ecology (Legendre and Fortin, 1989; Lennon, 2000). This positive spatial autocorrelation influences key mutualism properties in our simulated plant and seed-eating pollinator community. Here we show that the autocorrelation of habitat can affect mutualistic interactions in ways that may be counterintuitive. For example, low habitat autocorrelation can reduce the ability

of pollinators to find new plants. And while this leaves some plants without any reproductive output for one season, the reduction in pollinator search efficiency can also lead to a net gain in the probability that a plant will produce a seed by lowering the effective rate of pollinator oviposition. The implications of these results may be relevant to studies of seed-eating mutualisms, wherein much focus has been devoted to understanding how long-term stability is maintained when mutualist partners experience asymmetric fitness benefits from pollinator and seed production (e.g., Bronstein, 2001; Holland et al., 2002). Fitness costs and benefits are often determined by the measure of seed production in these systems. Because measurement of seed production is straightforward and easy to interpret comparatively among systems, seed-eating mutualisms have been recognized as the centerpiece of our understanding of the costs associated with mutualism (Bronstein, 2001). The proportion of flowers that develop into seeds can vary greatly in plant populations associated with seed-eating pollinators (e.g., Addicott, 1986; Pellmyr, 1989). We suggest that the autocorrelation of habitat may play an influential role in determining seed and pollinator production, thus affecting the costs and benefits of mutualism for both plant and pollinator.

In the absence of habitat autocorrelation ($\beta = 0$), the general pattern of patchy plant distribution in the presence of relatively long distance exploiter dispersal that Wilson et al. (2003) observed on a uniform landscape was also observed in our model (Supplemental Material S1). This result shows that the spatial dynamics of interacting mutualists and exploiters are robust to habitat heterogeneity. This robustness to non-uniform habitat is an important result that reinforces the applicability of previous plant-pollinator-exploiter models in light of more realistic landscape properties (e.g., Wilson et al., 2003; Morris et al., 2003; Bronstein et al., 2003). The emergence of patchiness with landscape non-uniformity is attributable to the same processes that occur on a uniform landscape as in Wilson et al. (2003). As plants disperse short distances to new areas

of unoccupied habitat, exploiters with long distance dispersal are able to rapidly invade and block the expansion of mutualists. That this general spatial distribution pattern of mutualists and exploiters persists in the presence of habitat heterogeneity is different than spatial patterns observed in some other community models. For example, Hassell et al. (1991) and Comins et al. (1992) modeled a uniform landscape with spatially explicit subpopulations of hosts and parasitoids connected by diffusive dispersal; they found emergent spatial patterns such as spiral waves or crystal lattices, but only a small amount of environmental heterogeneity is needed to destroy the spatio-temporal synchrony upon which these results depend (Singh et al., 2004; Hirzel et al., 2007). The resilience of spatio-temporal processes to habitat heterogeneity in our plant-pollinator-exploiter model reaffirm the prediction of spatial patchiness in mutualisms that include a relatively long dispersing species of exploiter.

The autocorrelation of plant habitat strongly affects the susceptibility of the mutualism to exploitation. Because exploiters oviposit into flowers that pollinators have visited and pollinated, but not used for oviposition, the persistence of exploiters depends on the number of pollinator visits that plants receive in a season. Pollinator visitation increases with habitat autocorrelation, especially when pollinator dispersal distance is low and pollinators are more likely to visit nearby cells on the landscape. When pollinators visit more flowers, more plants are both pollinated and used for pollinator oviposition. When the number of pollinator visits per flower is high, exploiters competing for pollinated flowers are competitively excluded. When the number of pollinator visits per flower is lower, in contrast, we find an increase in the mean number of flowers pollinated but not used for pollinator oviposition. In the absence of exploiters, this results in lower pollinator production and higher seed production, but when exploiters are present, the high proportion of pollinated flowers makes the mutualism more susceptible to exploitation. Our observations are consistent with previous models of mutualisms that include an ex-

exploiter species. In an analytical model of a plant and seed-eating pollinator, Morris et al. (2003) found high pollinator densities to lower seed production, leading to a feedback loop that ultimately prevents pollinators from over-exploiting plant resources, which would otherwise cause the extinction of both mutualists. Upon including exploiters, which compete with pollinators for access to plant resources, coexistence is possible as long as the birthrate of pollinators lies between two extremes relative to the birthrate of exploiters. When pollinator birthrate is too high, it becomes more difficult for exploiters to achieve positive growth and persist in the community. In contrast, when pollinator birthrate is low, exploiters can increase to high densities and drive both mutualists (and themselves, in turn) to extinction. Our results show that these dynamics are sensitive to habitat heterogeneity and the spatial arrangement of habitat on a landscape. When high habitat autocorrelation leads to the aggregation of plants, the number of pollinator visits per flower increases (Figure 4c). The increase in pollinator visits per flower and subsequent increase in pollinator production is enough for habitat autocorrelation alone to lead to the competitive exclusion of exploiters for many demographic values (Figure 6). In turn, when exploitation is sufficiently high to lead to the extinction of all three species at low habitat autocorrelations, higher levels of habitat autocorrelation increase the number of pollinator visits per flower and reduce exploitation rates, leading to long-term coexistence.

We noticed another pattern of plant spatio-temporal patchiness in simulations with positive habitat autocorrelation that either did not include exploiters, or in which exploiters were competitively excluded by pollinators very early in the simulations. As with pollinator production, seed production, and global mutualist densities, this spatio-temporal patchiness was driven by the mean number of pollinators plants received during a season. As the mean number of pollinator visits increased, the probability of seeds being produced in areas wherein pollinators were most aggregated became vanishingly

small, and plants in these areas were much more likely to produce pollinators instead of seeds. At high habitat autocorrelation, the centers of large habitat patches were areas in which the mean pollinator visits per flower were especially high. As a result, pollinator production was higher in these regions, leading to spatial segregation in plants that produced pollinators versus plants that produced seeds. Large habitat patches often contained subpatches in which plants were sparse or entirely absent because no nearby plants were producing seeds. In simulations with high habitat autocorrelation, plant distribution was most dense toward the outer edges of large habitat patches because pollinator visits around edges were less frequent than visits to patch centers, which received pollinators from every direction. This resulted in localized variability in seed and pollinator production among plants, with pollinator production being more likely in regions wherein plants and pollinators aggregated, and seed production being more likely in regions wherein pollinator dispersal limitation led to low mean numbers of pollinator visits. Predictably, as pollinator dispersal distance increased, the scale of this variability increased too. Relatively long distance pollinator dispersal resulted in lower turnover of pollinator versus seed production on the landscape (Supplemental Material S1). When dispersal is unlimited, all cells are effectively spatially equivalent, and no turnover occurs. In sum, our model shows how the autocorrelation of habitat combined with limited dispersal leads to spatial variation in pollinator visits to plants and ultimately the costs and benefits of mutualistic interactions. This relationship is likely to be further complicated in real world plant-pollinator mutualisms. In our model, plants produce a single ovule, which is sufficiently pollinated by the arrival of a single pollinator. For empirical systems in which plants rely on seed-eating pollinators, multiple ovules exist on a single plant, and multiple visits from pollinators may result in increased pollination in addition to an increase in seed predation. For example, in the mutualism between the perennial herb *Trollius europaeus* and its pollinating and seed-eating *Chiastocheta* flies, repeated

pollinator visits lead to increasing, but diminishing, pollination efficacy (Pellmyr, 1989). And because pollinator larvae in this mutualism feed on multiple developing seeds, plants with especially frequent pollinator visits suffer a net reproductive loss (Pellmyr, 1989).

Empirical studies of other seed-eating mutualisms suggest that spatial dynamics are important to consider when interpreting ecological patterns. In a study of *Tegeticula yuccasella*, the seed-eating pollinator of *Yucca filamentosa*, dispersal was observed to be highly leptokurtic – much pollination was observed on the same plant from which pollinators developed (Marr et al., 2000). Rarely, pollinators were observed dispersing as far as 50 meters, but the average distance for pollen transfer was 4.66 meters. The distribution of pollinator dispersal in our model was similarly leptokurtic. Cell inspection for a pollinator with short distance dispersal was on average a distance of ca 2.7 cells away from the cell at which it began at the start of a season (ca 11.8 cells away for pollinators with long distance dispersal). If we consider each cell of our model to represent an area of roughly 2×2 meters, our model predicts significant, spatially correlated, variation in pollinator and seed production at the within population level of *Y. filamentosa*. In a study of eight species of *Yucca*, Addicott (1986) observed high variation in seed and pollinator production within populations. Addicott suggested the mean number of pollinator visits could be influential in explaining this variation, but did not explicitly consider the spatial autocorrelation of plants within a population. Addicott (1986) further suggested the high variation observed in seed production to be evidence against the hypothesis that there is strong regulation of yucca-yucca moth interaction. Here we show that this need not be the case; both strong population regulation and high variation in pollinator and seed production are expected when habitat is autocorrelated (Supplemental Material S1). Given the high pollinator and seed production variation observed in similar systems, such as those of figs and their pollinating wasps (e.g., Bronstein and Hossaert-McKey, 1996) or globeflowers and their pollinating flies (e.g., Després et al., 2007), our results

may be useful for interpreting ecological patterns in these communities. In the context of mutualistic interactions between plants and their seed eating pollinators, spatial variation in pollinator and seed production may also be relevant given that pollinators represent the male fitness of plants, while seeds represent female plant fitness. It would be interesting to consider the influence of habitat autocorrelation and pollinator visits per flower on the mating strategies of seed plants. Because pollinator production in our model was very high relative to seed production in the centers of large habitat patches, plants in these regions producing seeds may be expected to have especially high fitness due to the high probability of successful pollination and seed establishment. In contrast, the more common pollinator producing plants in these regions would be expected to have especially low fitness due to the lower mean reproductive success caused by intense competition among local pollinators for access to ovules.

Our model shows the potential complexities involved in understanding the ecological dynamics of even simple three species communities. In a classic plant-pollinator mutualism that includes an exploiter species, relatively small changes in the spatial autocorrelation of habitat may cause substantial changes in community dynamics. Further, Jones et al. (2009) suggest that environmental heterogeneity may influence coevolutionary dynamics in such systems, and that metapopulations of mutualists and exploiters may be evolutionarily stabilized if populations differ in their evolutionary stages. While the impact of environmental autocorrelation on ecological processes is still not fully understood (Schiegg, 2003), empirical studies show that it can have important effects on population dynamics (e.g., González-megías et al., 2005; Schooley and Branch, 2007; Trenham et al., 2001). We suggest that environmental autocorrelation may similarly influence the ecology and evolution of model communities of mutualists that include seed-eating exploiters.

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Parameter	Description	Default Value
Δ_P	Plant (seed) dispersal distance	2
Δ_M	Mutualist pollinator dispersal distance	2
Δ_E	Exploiter dispersal distance	2
δ_P	Plant mortality probability	0.02
δ_M	Mutualist pollinator mortality probability	0.2
δ_E	Exploiter mortality probability	0.2
γ	Mutualist pollinator oviposition probability	0.5
η	Mutualist pollinator cell inspection rate	6
ε	Exploiter cell inspection rate	15
θ	Plant ovulation probability	1.0

Table 1: Default parameter values for an individual-based model of plant, pollinator, and exploiter interactions on a spatially explicit landscape.

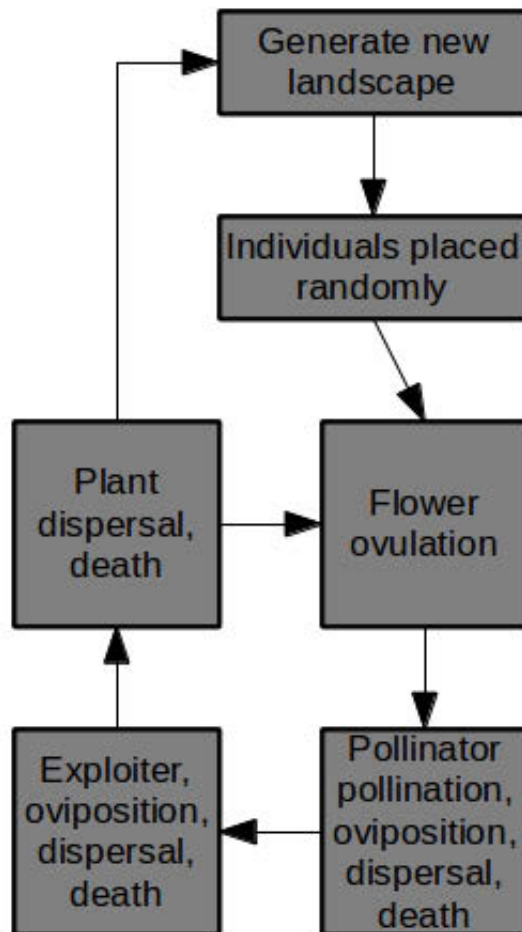


Figure 1: Interactions among plants, obligate pollinators, and obligate exploiters for a single set of parameter values.

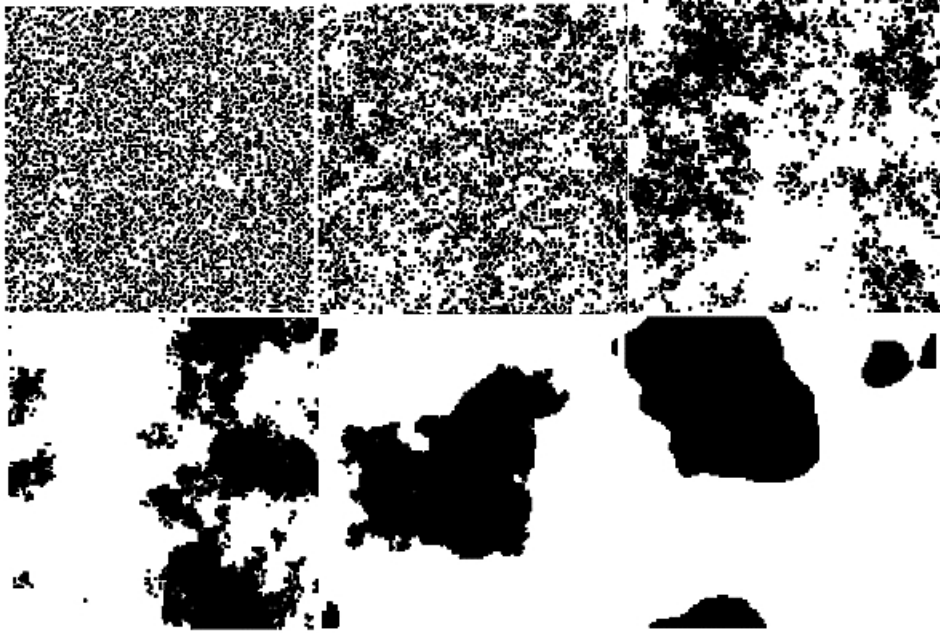


Figure 2: Different levels of habitat autocorrelation on a landscape constructed with a power spectrum function. Autocorrelation varies with different values of β . The values of β shown range from a random landscape to a highly autocorrelated landscape ($\beta = 0$, upper left; $\beta = 1$, upper middle; $\beta = 2$, upper right; $\beta = 3$, lower left; $\beta = 4$, lower middle; $\beta = 5$, bottom right).

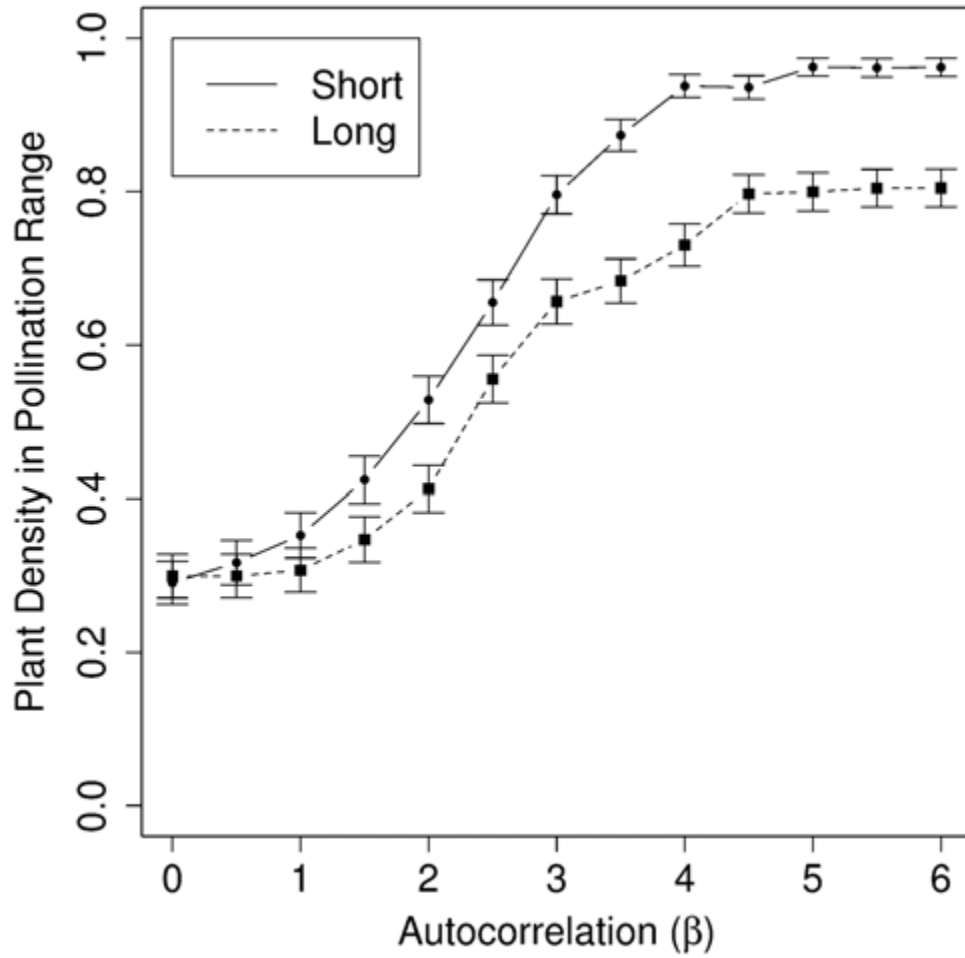


Figure 3: For a random habitable cell, the density of habitable cells on a landscape within the radius of maximum dispersal for an average short (ca 3.6 cells) and long (ca 15.7 cells) distance dispersing pollinator as a function of habitat autocorrelation values (β). Error bars reflect 95% confidence intervals around the means.

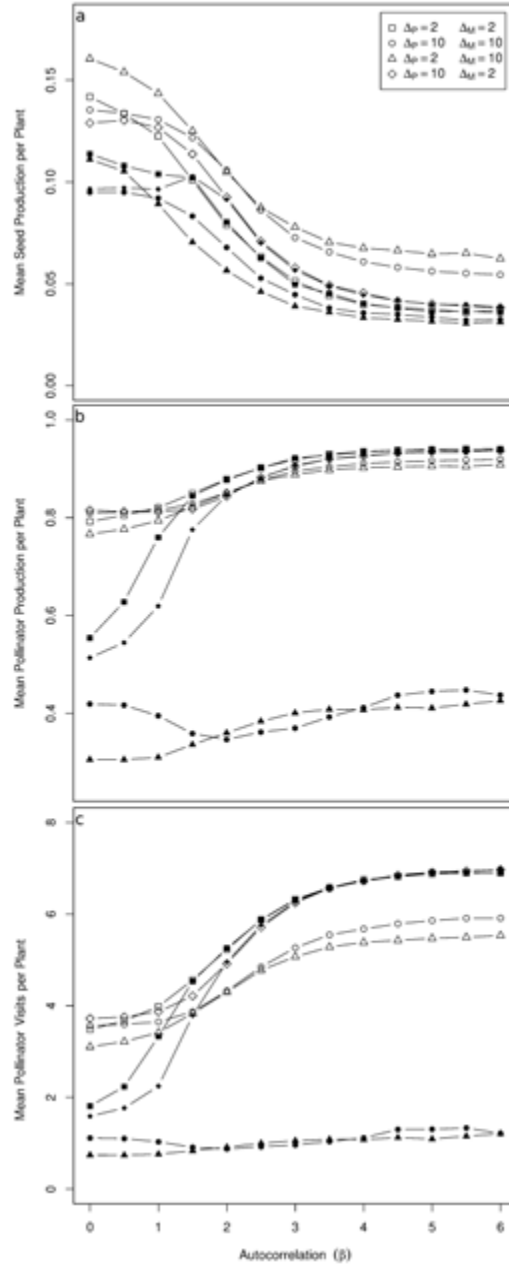


Figure 4: Mean seed production, pollinator production, and pollinator visits per plant as habitat autocorrelation increases. Unfilled symbols show simulations with different combinations of high (10) and low (2) plant dispersal Δ_P and pollinator dispersal Δ_M in the absence of exploiters. Simulations with exploiters included (always with low dispersal) are shown with filled symbols.

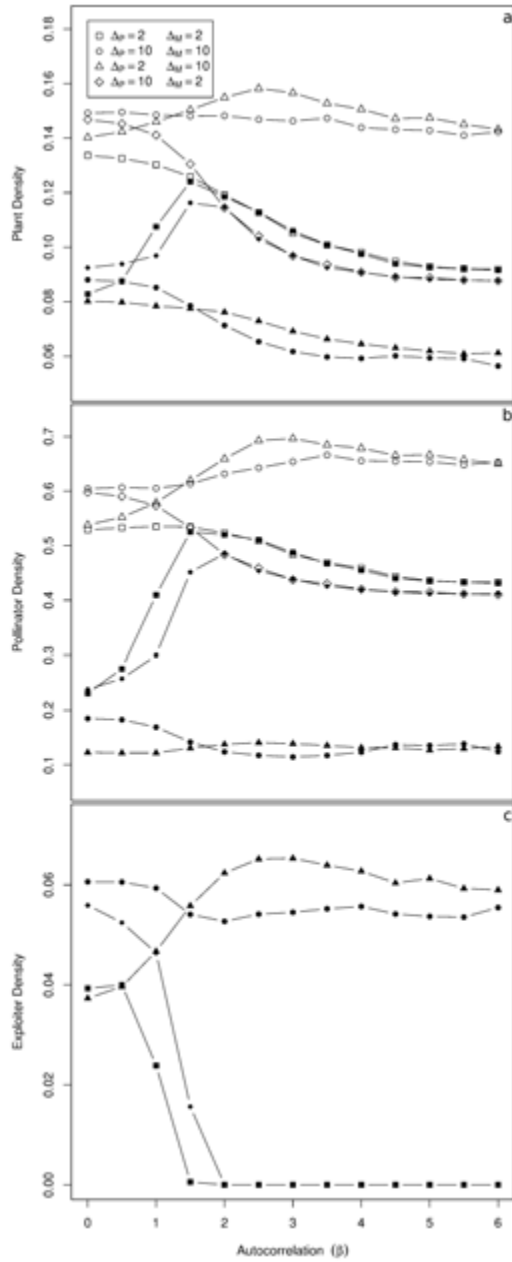


Figure 5: Mean plant, pollinator, and exploiter density as habitat autocorrelation increases. Unfilled symbols show simulations with different combinations of high (10) and low (2) plant dispersal Δ_P and pollinator dispersal Δ_M in the absence of exploiters. Simulations with exploiters included (low dispersal) are shown with filled symbols.

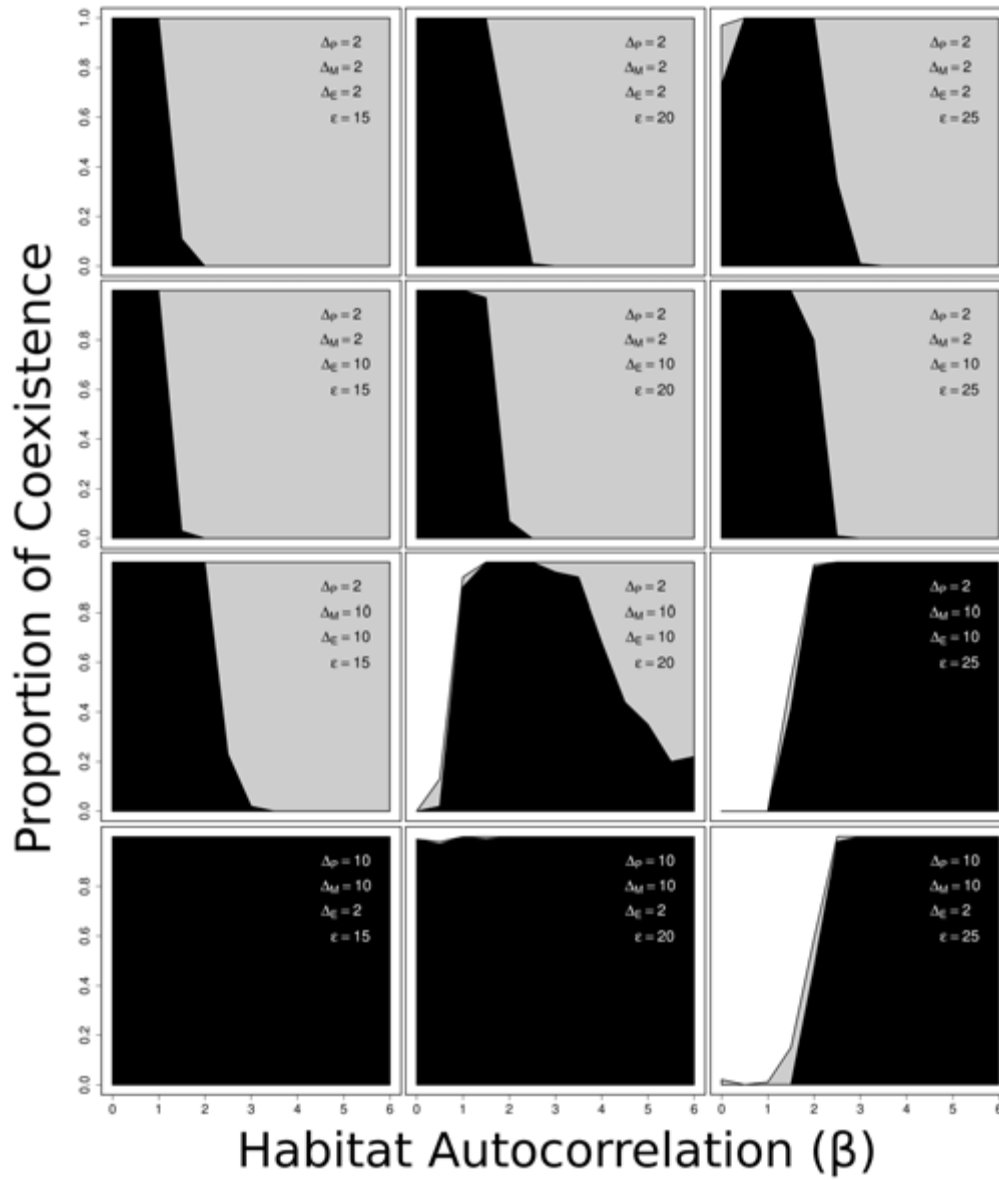


Figure 6: Results of different dispersal and exploiter cell inspection rates at different levels of habitat autocorrelation on community coexistence. Rows show different dispersal combinations in plants, pollinators, and exploiters. Columns show simulations of different levels of exploiter cell inspection rates. The x-axis of each graph within the figure shows habitat autocorrelation ranging from no autocorrelation ($\beta = 0$) to high autocorrelation ($\beta = 6$). The y-axis of each graph shows the proportion of simulations that lead to one of three results: long-term coexistence of mutualists and exploiters (black), extinction of only the exploiter (gray), and extinction of all three species (white).

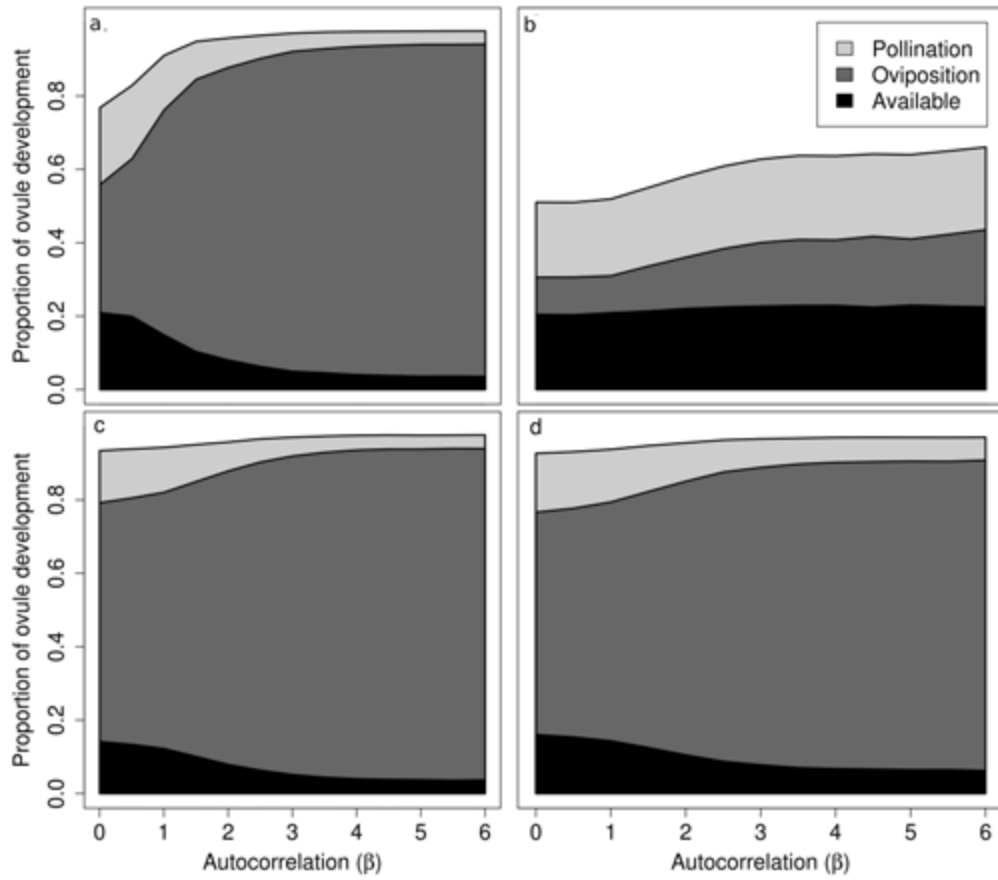


Figure 7: Proportion of plant ovules pollinated (light gray), used for oviposition by pollinators (dark gray), and remain available for either seed or exploiter development (black). Ovule proportions are shown at different levels of habitat autocorrelation with short (A) and long (B) distance pollinator dispersal in the presence of short dispersing exploiters, and with short (C) and long (D) distance pollinator dispersal in the absence of exploiters. Simulations in A consistently resulted in early exploiter extinction for values of $\beta \geq 2$.

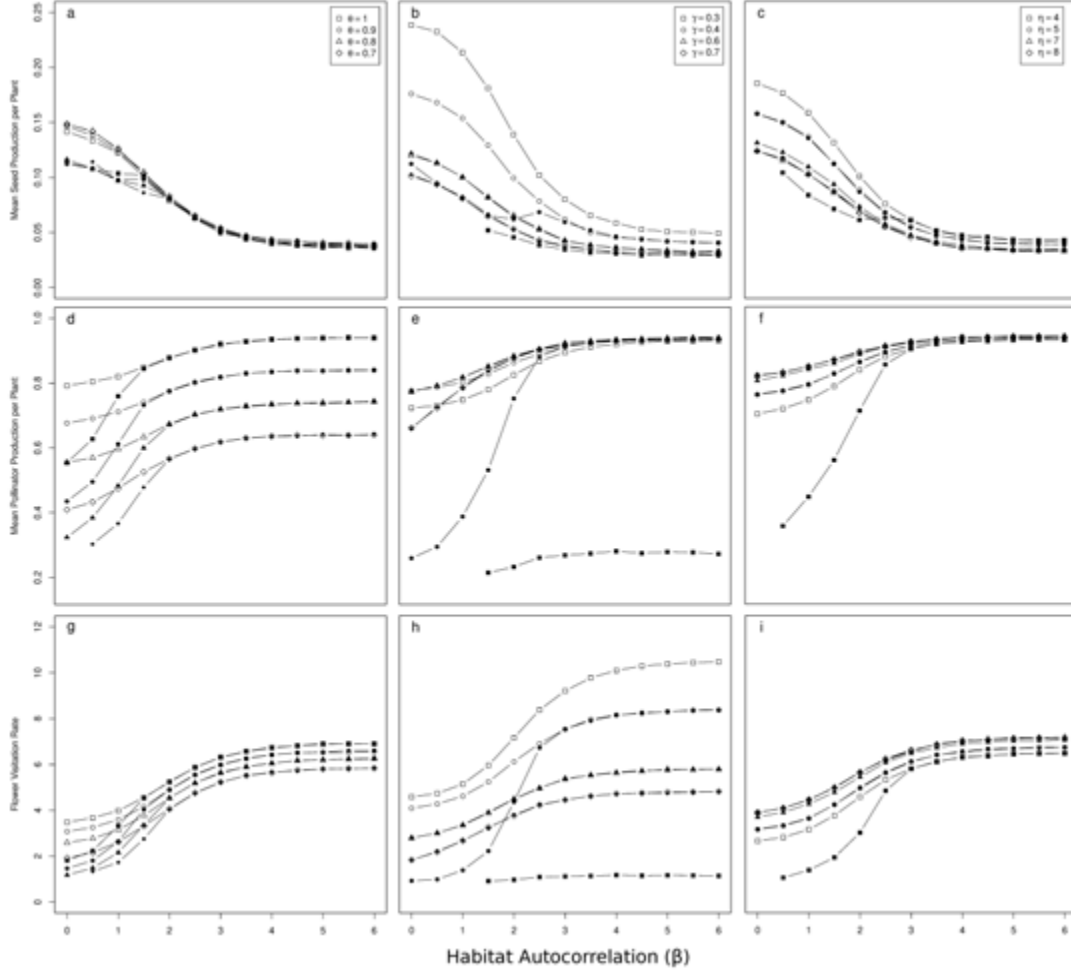


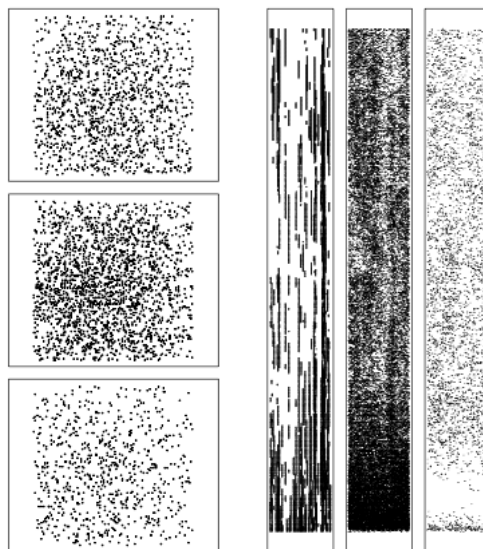
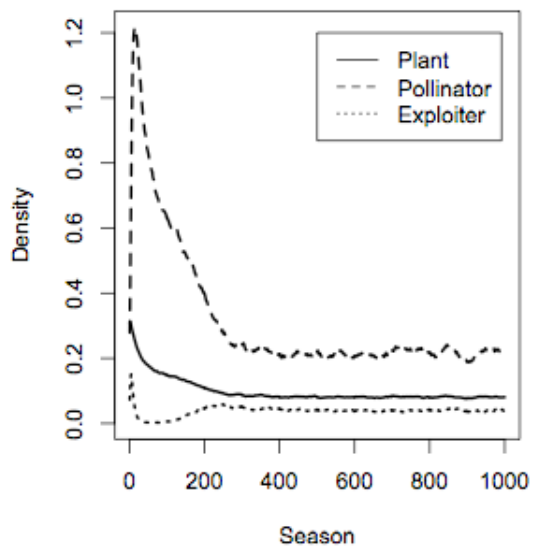
Figure 8: Effect of habitat autocorrelation on mean seed production, pollinator production, and flower visitation per plant at different values of flower ovulation probability (θ ; a, d, & g), pollinator oviposition probability (γ ; b, e, and h), and pollinator cell inspection rate (η ; c, f, & i). Unfilled symbols show simulations in the absence of exploiters; simulations with exploiters are shown with filled symbols.

8. Supplemental Information 1

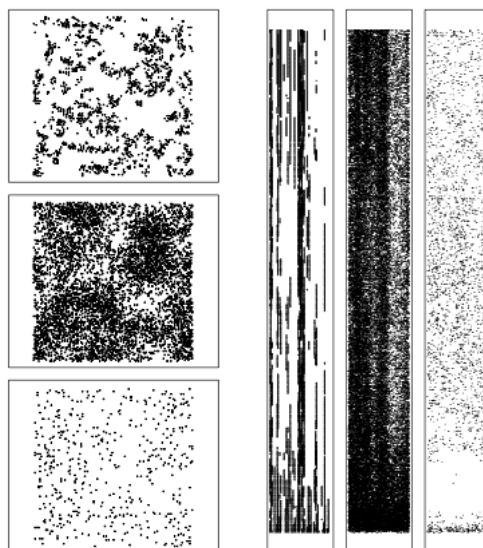
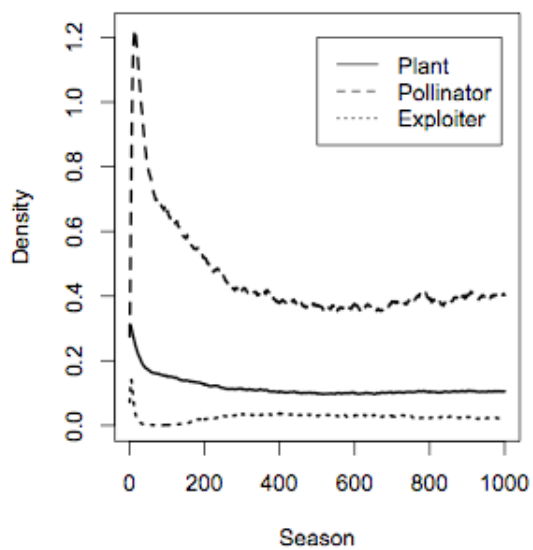
Note: This supplement displays changes in the densities of plants, seed-eating pollinators, and seed-eating exploiters on a simulated 128×128 landscape over a period of 1000 seasons at different levels of exploiter visitation rate and habitat autocorrelation. Square spatial images show the distributions of plants (top), pollinators (middle), and exploiters (bottom) after 500 seasons have passed. Vertical columns show space-time (XT) images of plants (left), pollinators (middle) and exploiters (right). These XT images show the densities of each species in a single transect of the 128×128 landscape from the start of each simulation (bottom) to the 1000th season (top). Below is a list of the simulations displayed in this supplemental material along with their corresponding page numbers.

Δ_P	Δ_M	Δ_E	β	ϵ	Page	Δ_P	Δ_M	Δ_E	β	ϵ	Page
2	2	2	0	15	51	2	10	10	0	20	60
2	2	2	1	15	51	2	10	10	1	20	61
2	2	2	2	15	52	2	10	10	2	20	61
2	2	2	3	15	52	2	10	10	3	20	62
2	2	2	4	15	53	2	10	10	4	20	62
2	2	2	5	15	53	2	10	10	5	20	63
2	2	2	6	15	54	2	10	10	6	20	63
2	2	2	0	20	54	2	10	10	0	25	64
2	2	2	0	25	55	2	10	10	1	25	64
2	2	2	1	25	55	2	10	10	2	25	65
2	2	2	2	25	56	2	10	10	3	25	65
2	2	2	3	25	56	10	10	2	0	15	66
2	2	10	0	15	57	10	10	2	3	15	66
2	2	10	1	15	57	10	10	2	6	15	67
2	2	10	2	15	58	10	10	2	0	25	67
2	10	10	0	15	58	10	10	2	1	25	68
2	10	10	1	15	59	10	10	2	2	25	68
2	10	10	2	15	59	10	10	2	3	25	69
2	10	10	3	15	60						

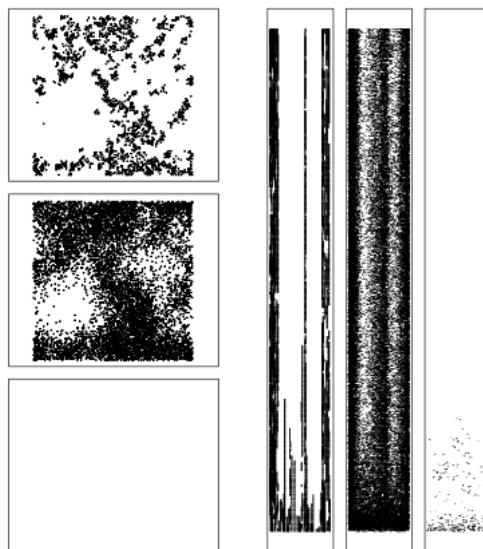
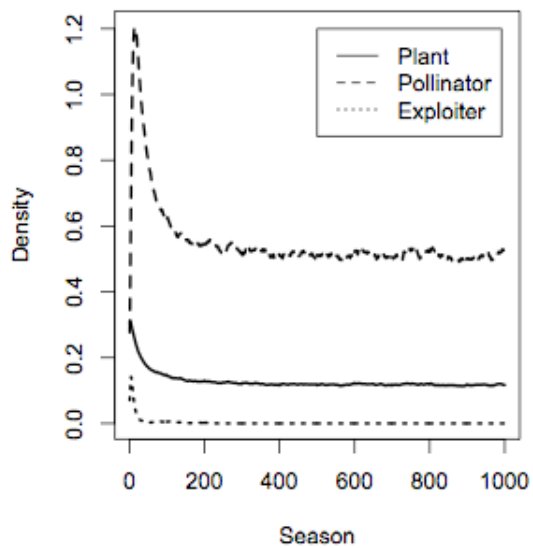
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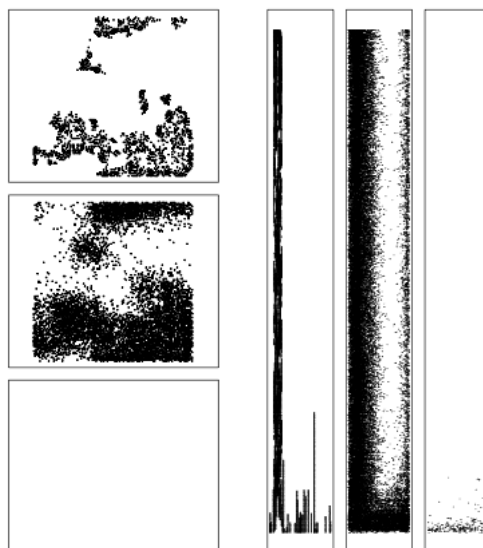
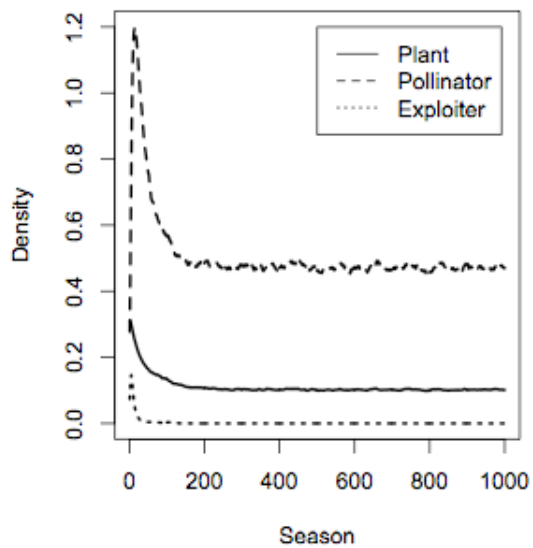
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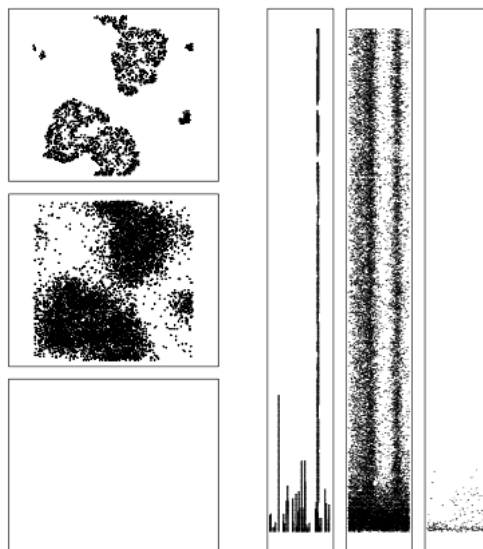
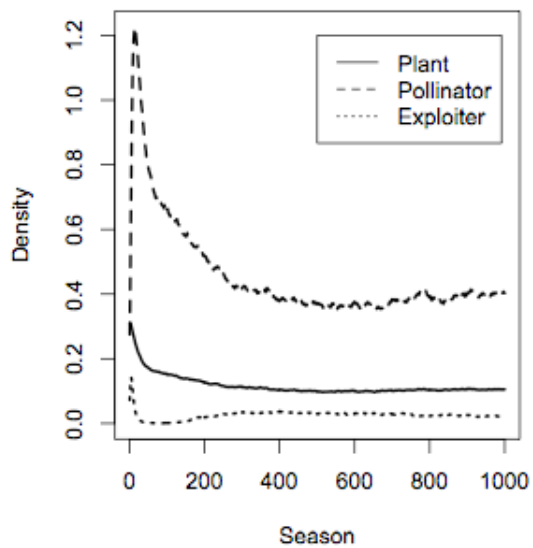
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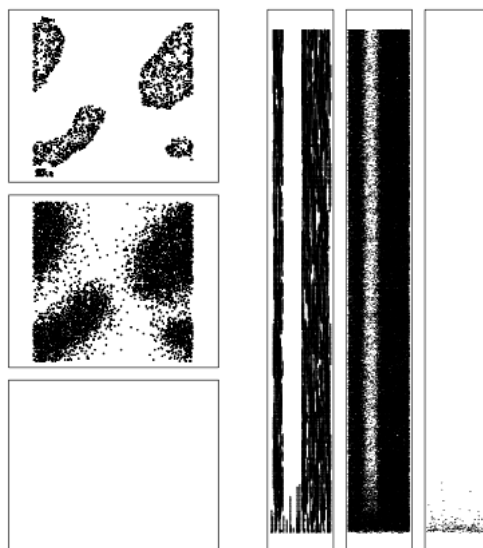
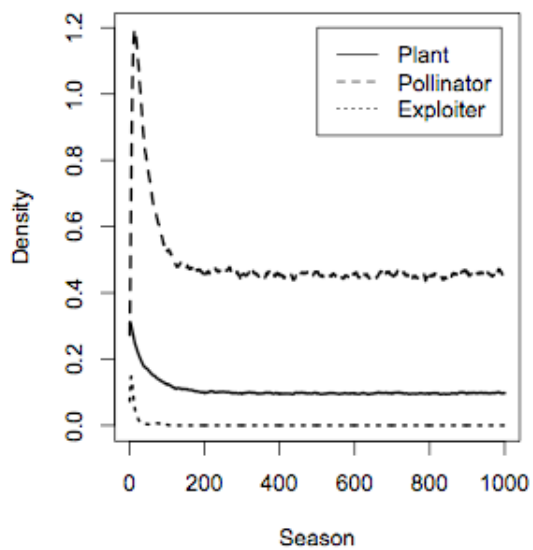
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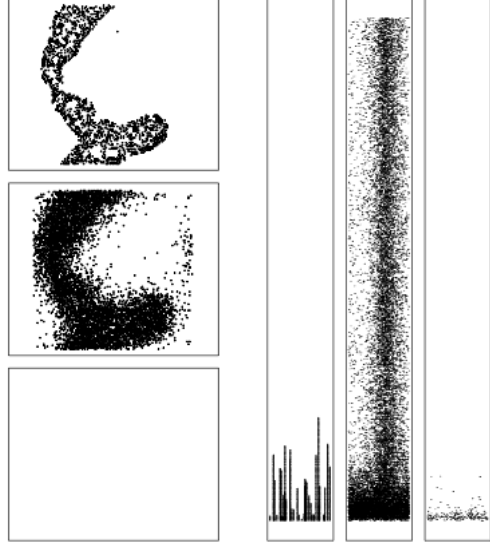
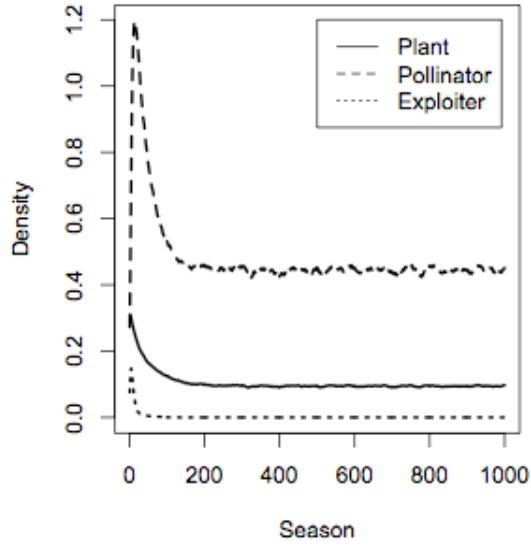
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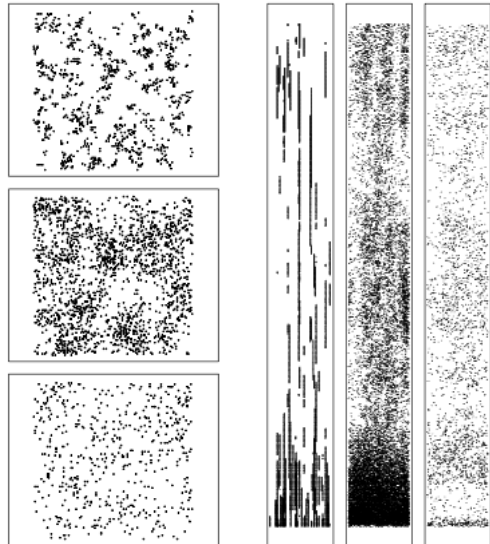
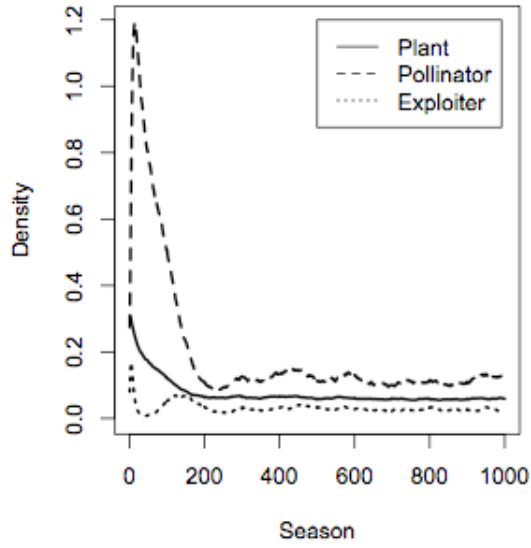
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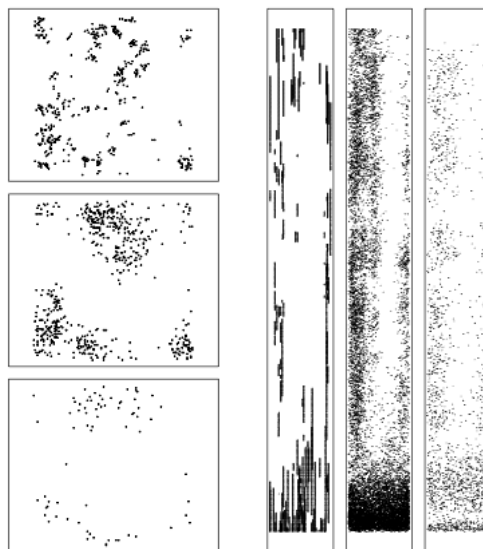
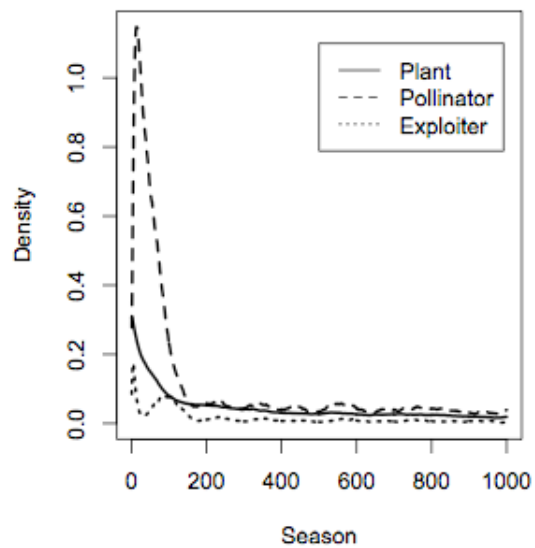
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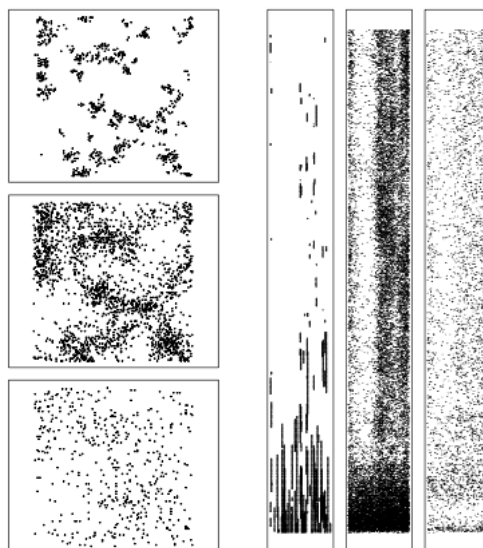
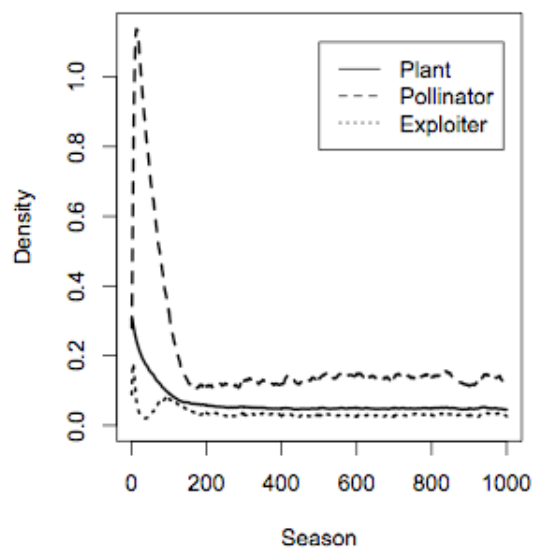
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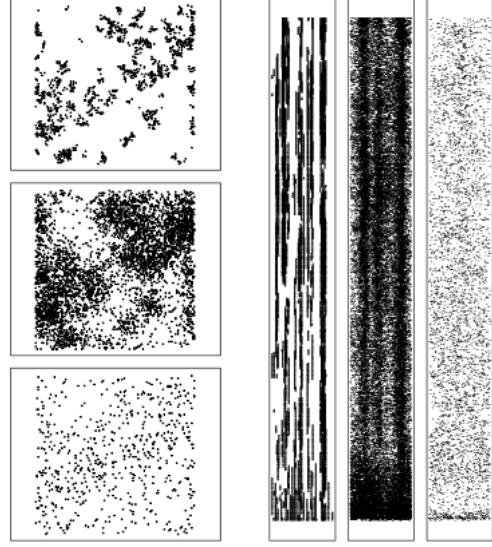
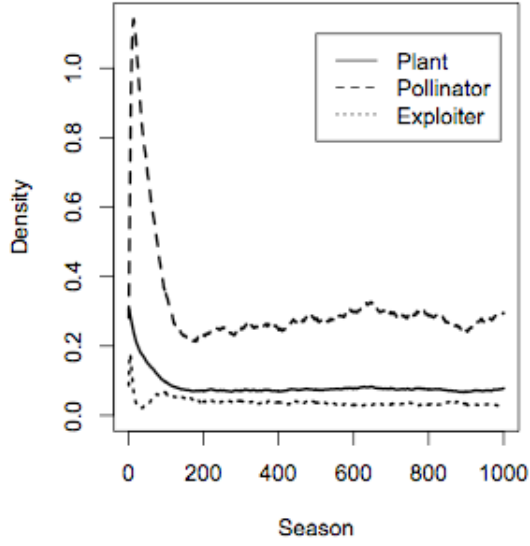
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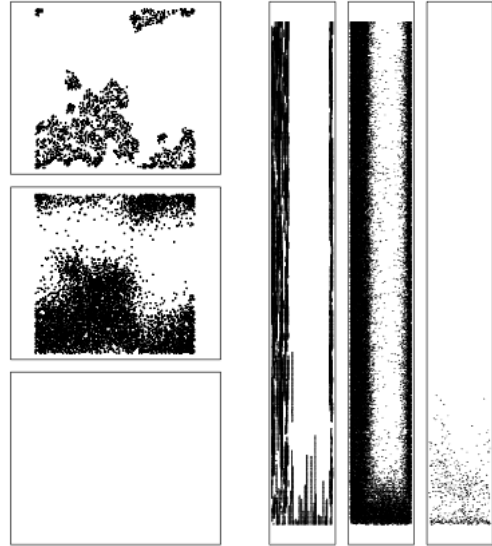
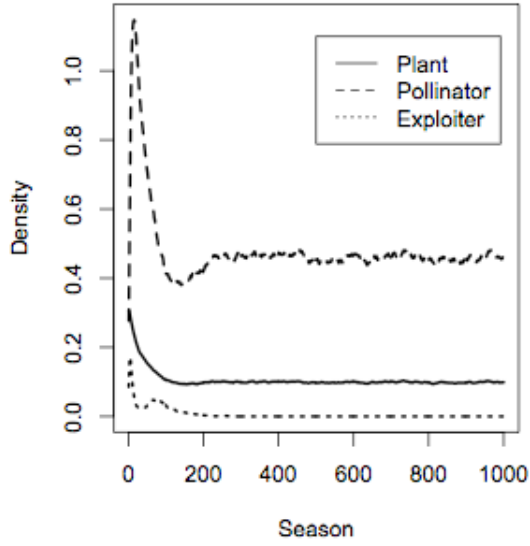
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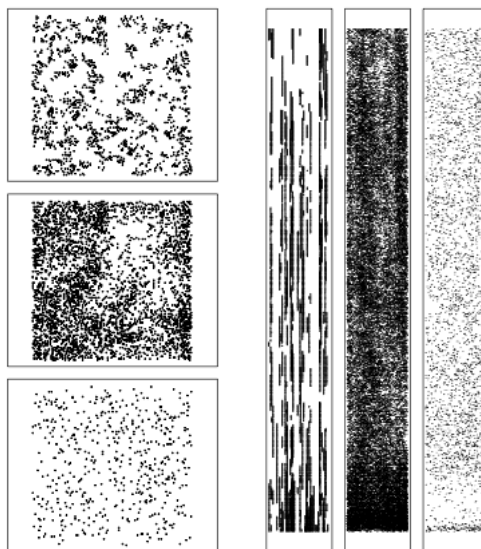
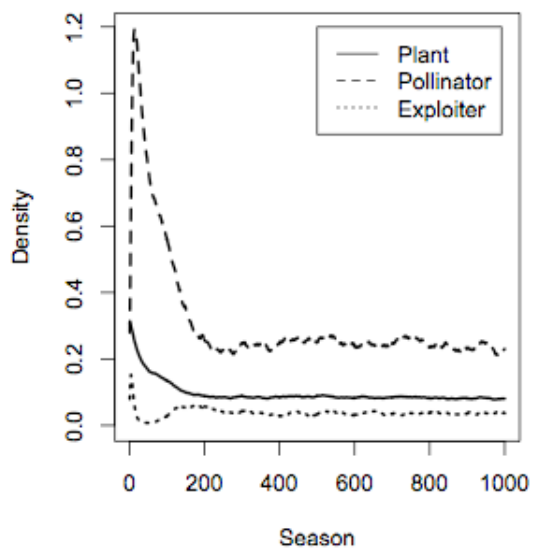
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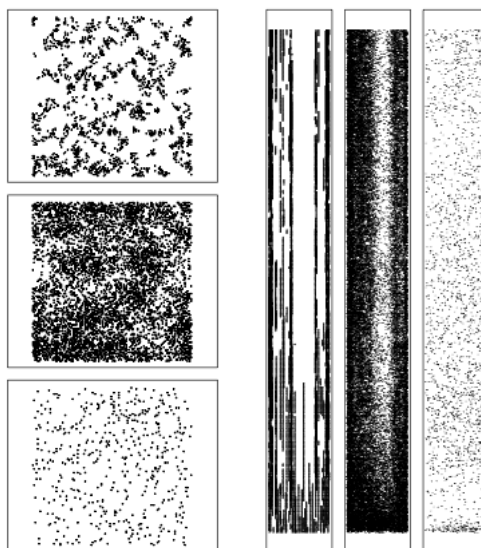
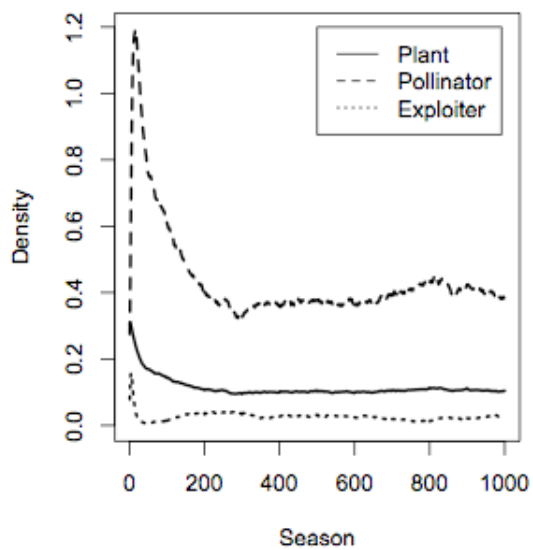
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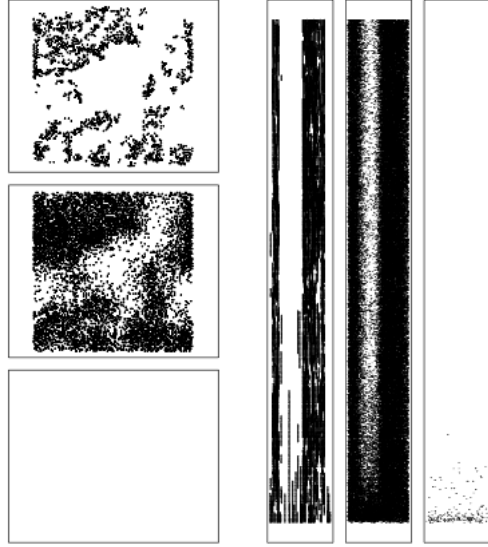
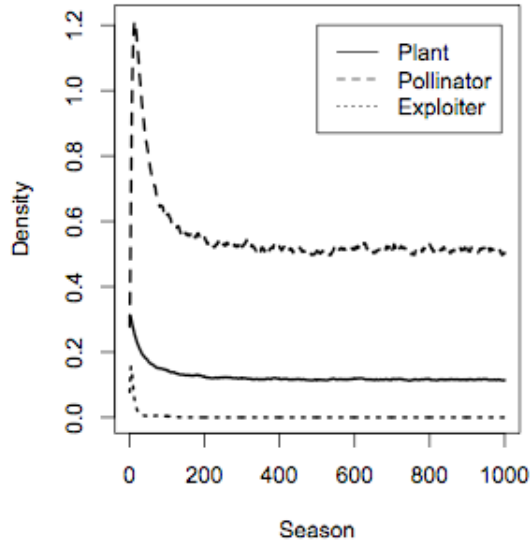
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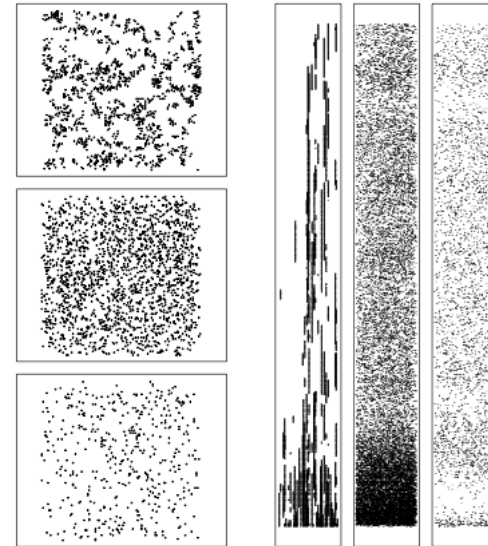
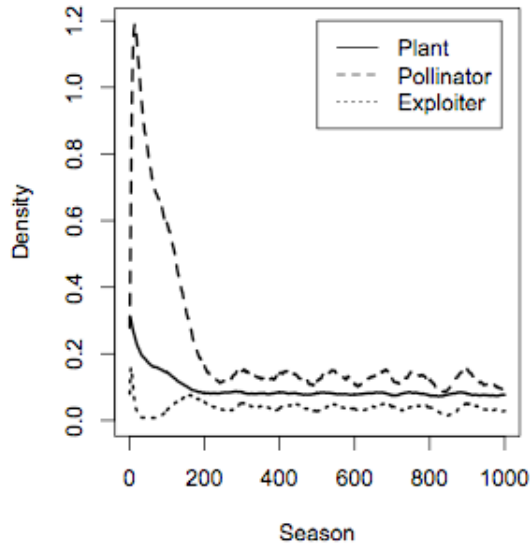
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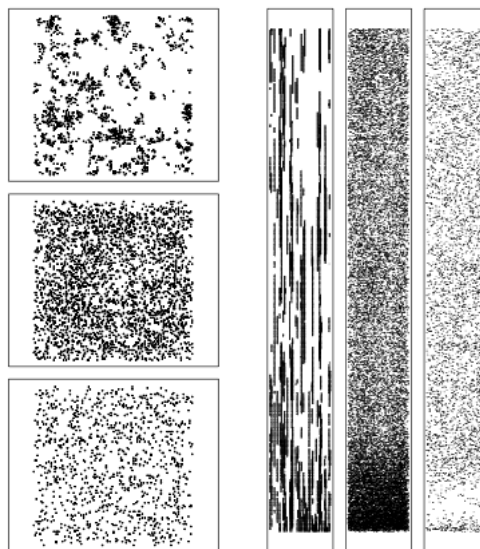
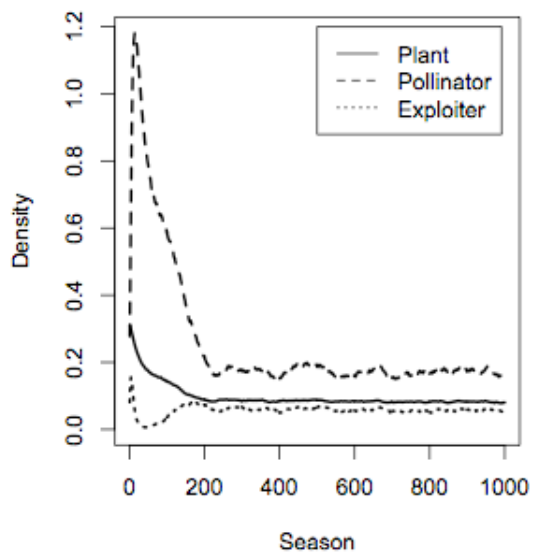
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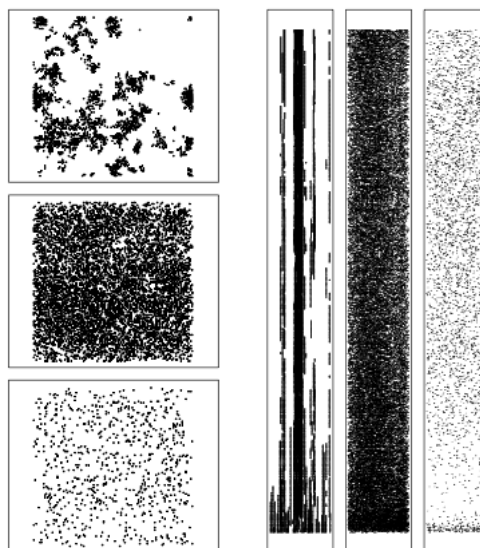
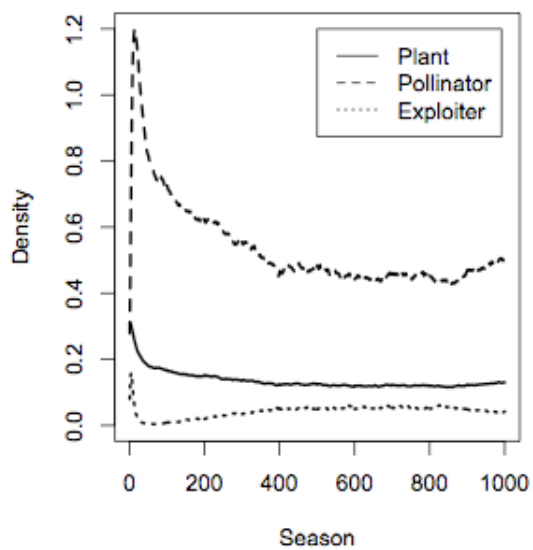
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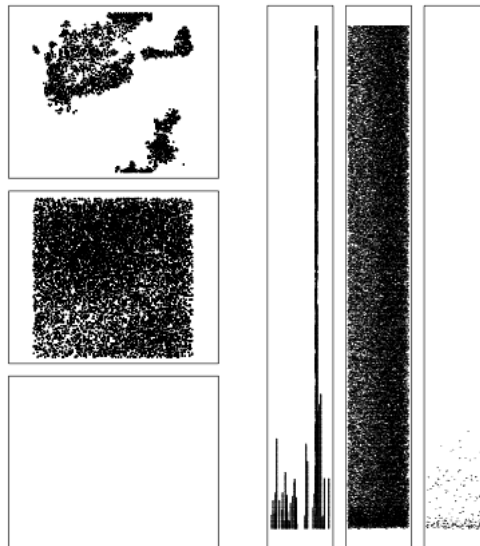
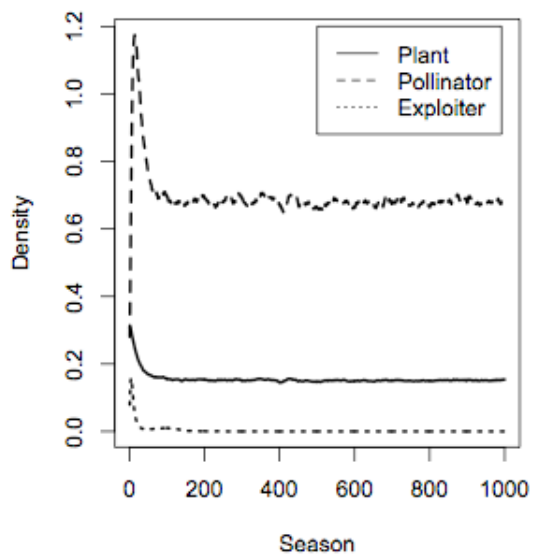
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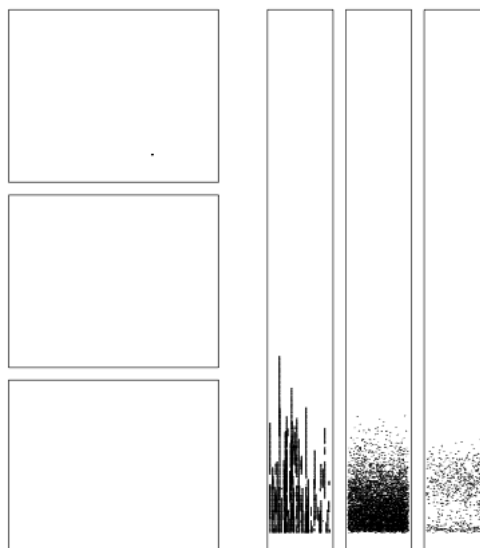
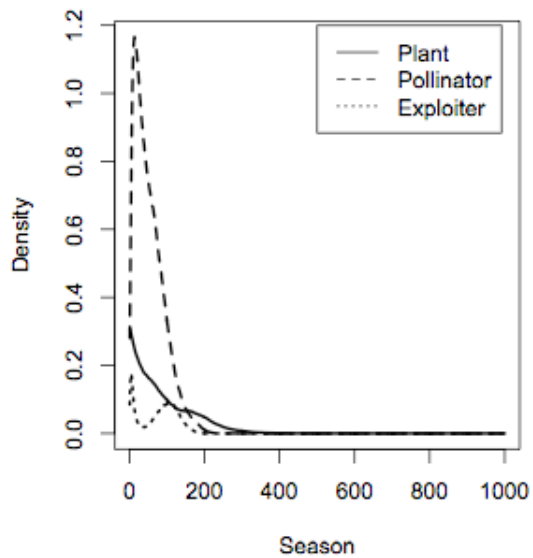
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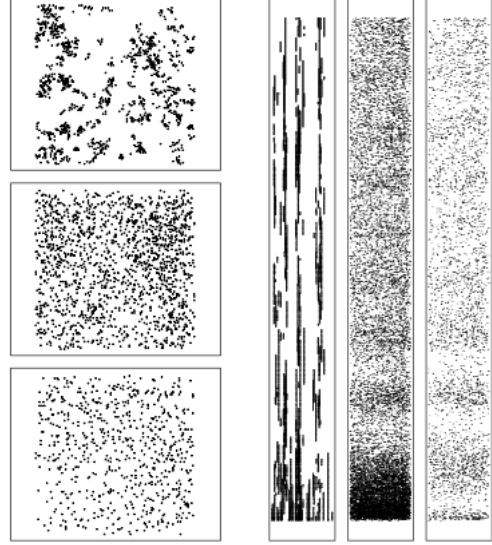
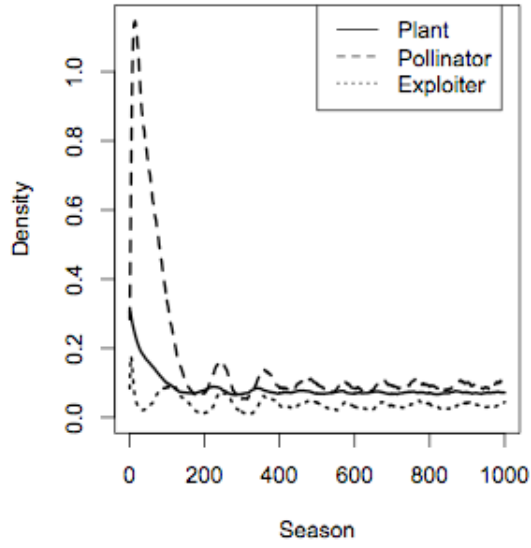
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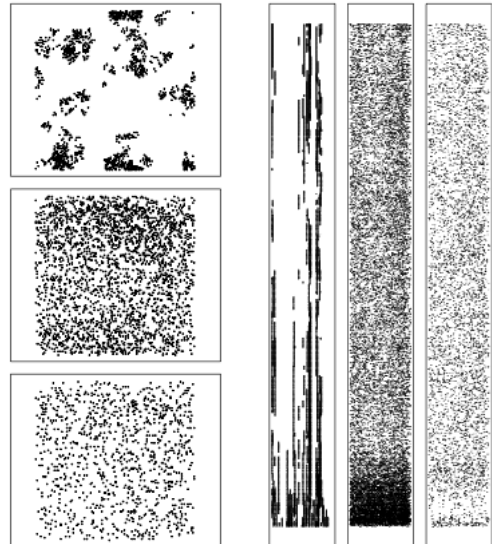
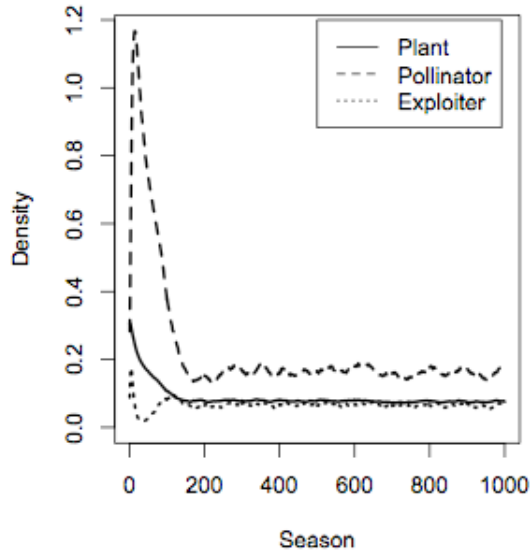
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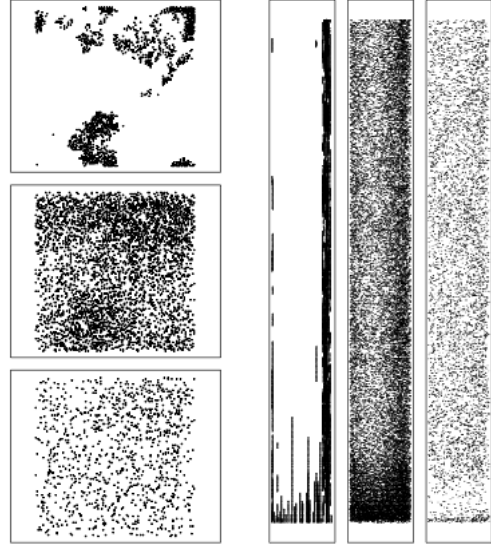
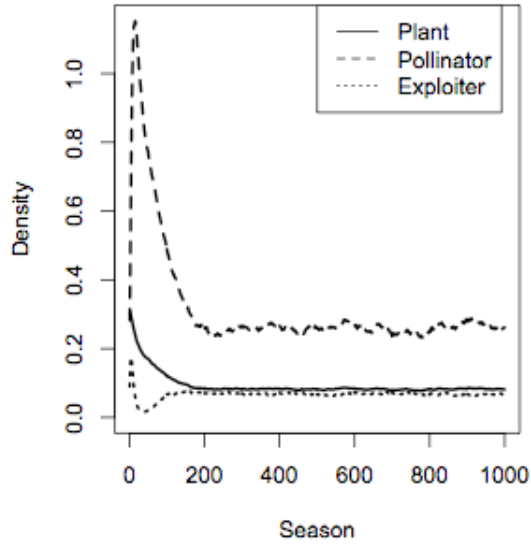
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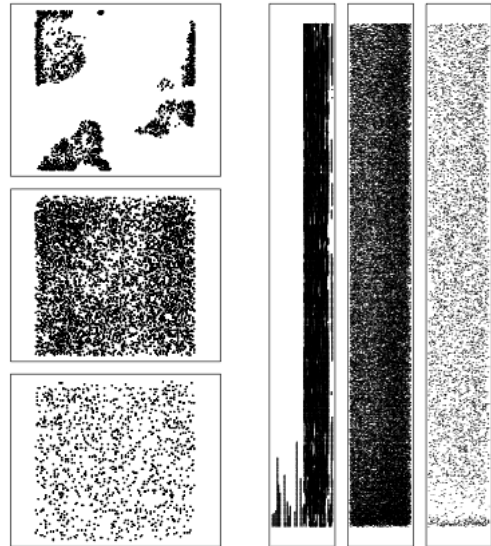
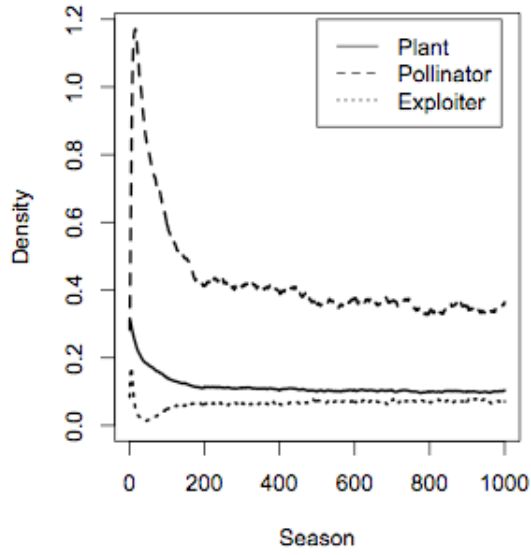
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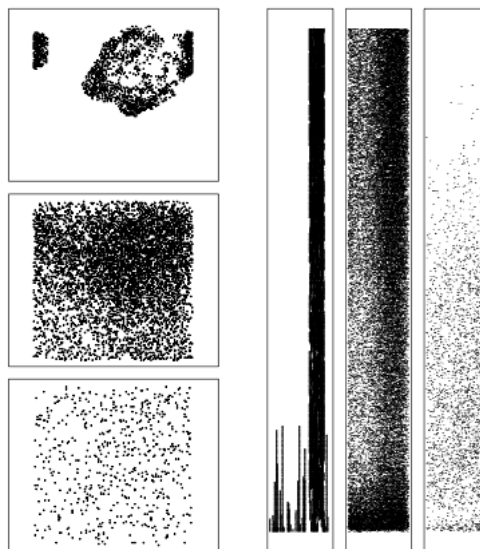
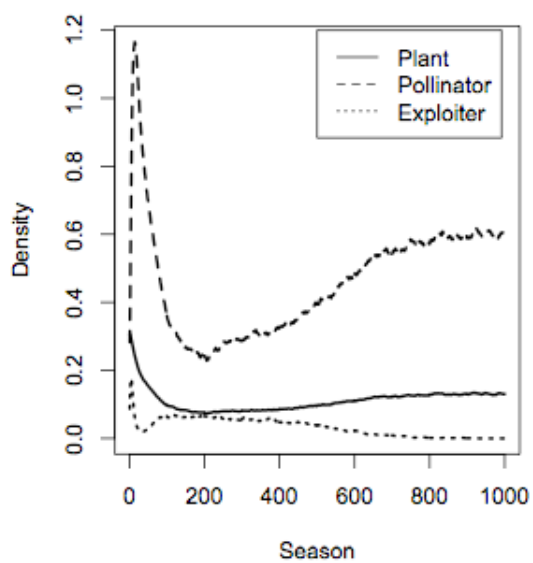
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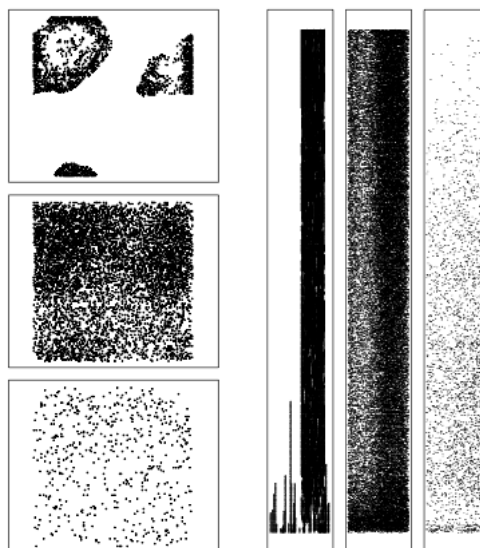
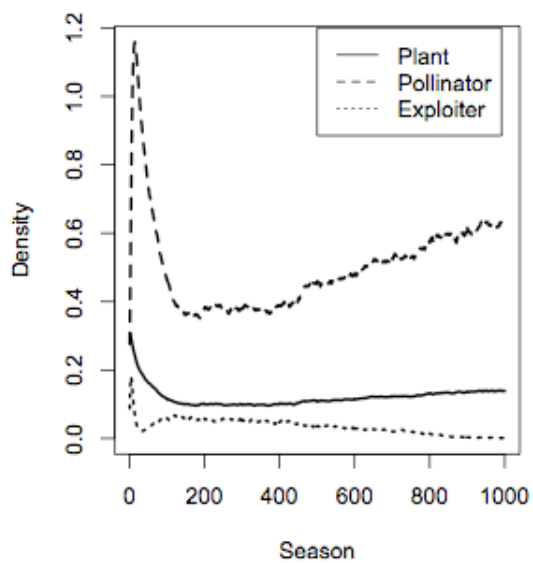
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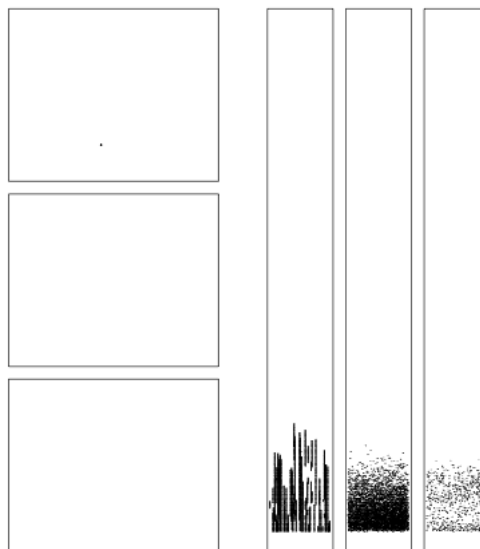
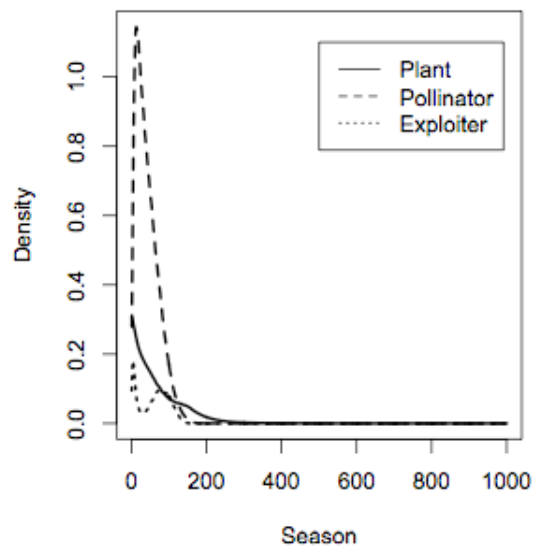
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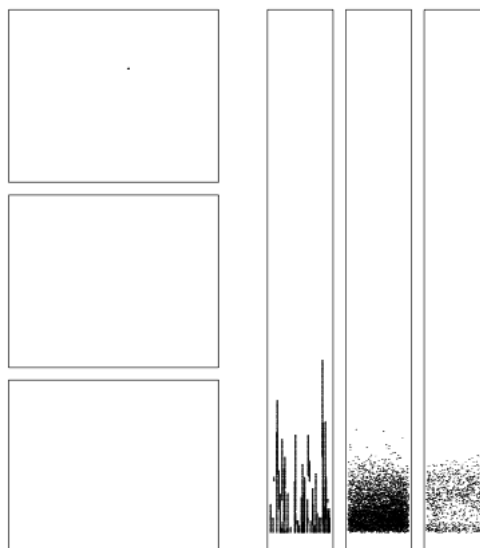
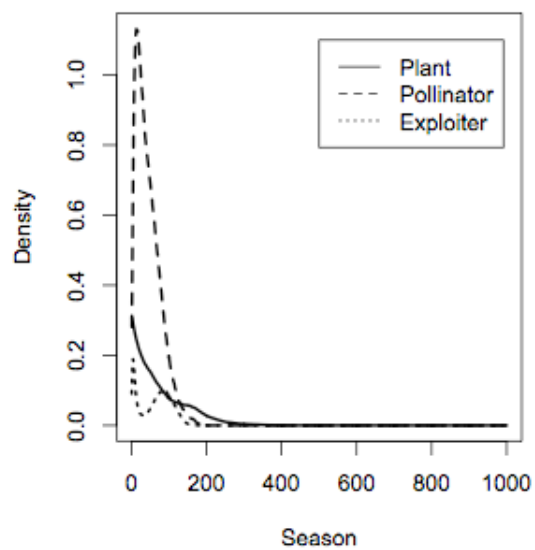
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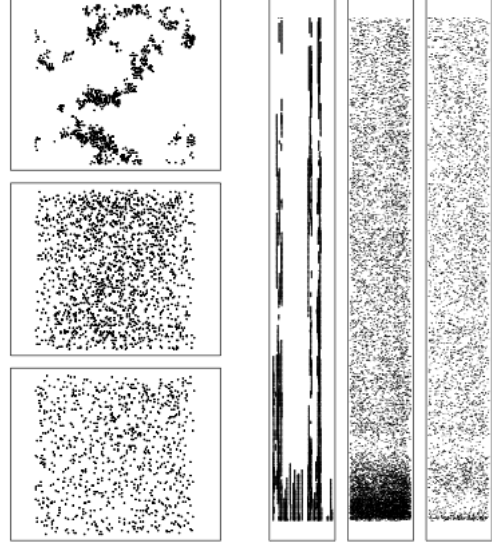
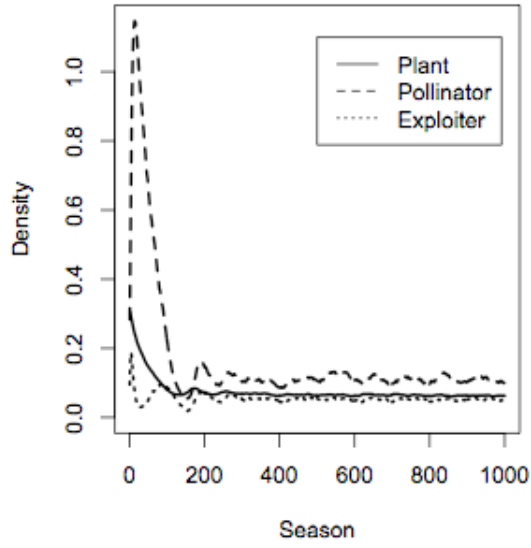
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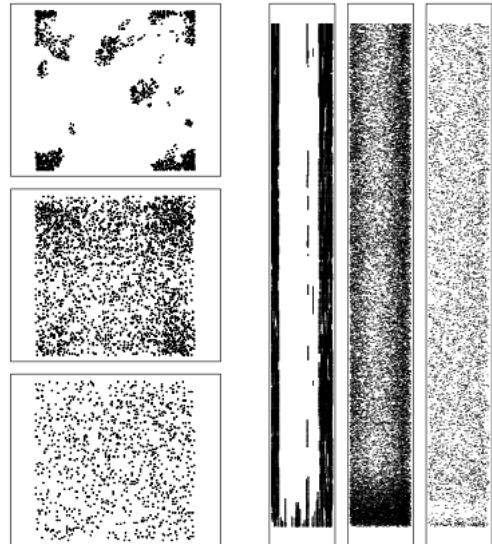
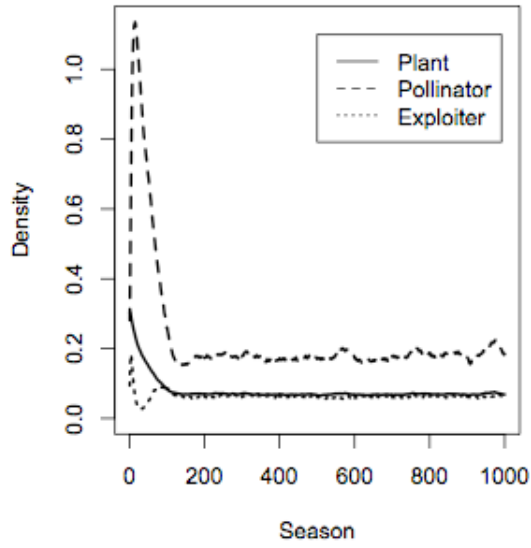
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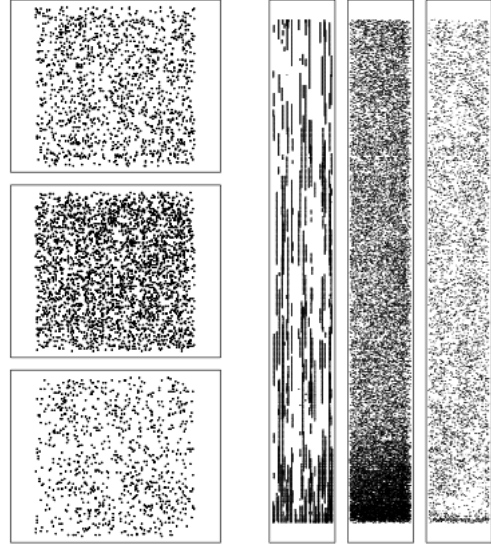
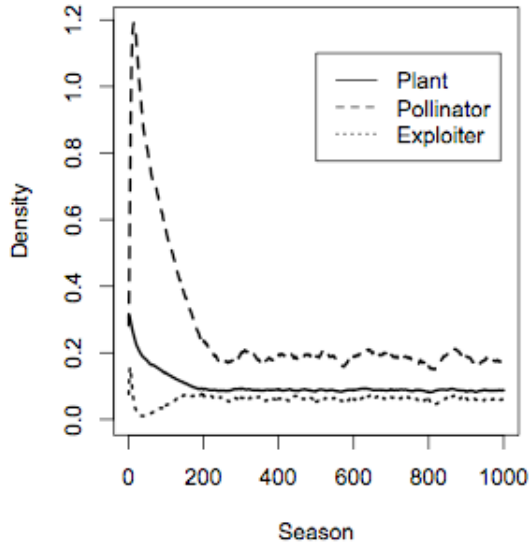
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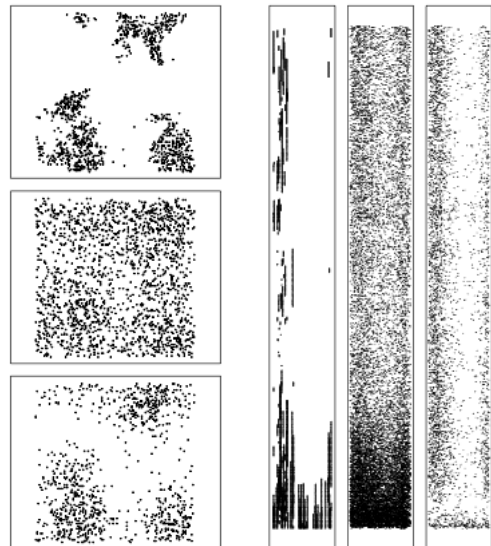
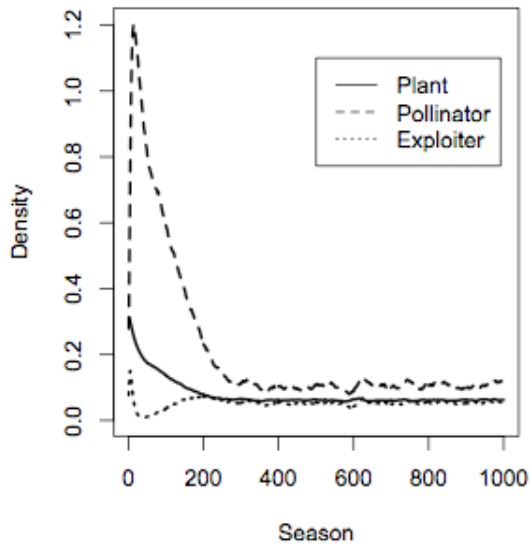
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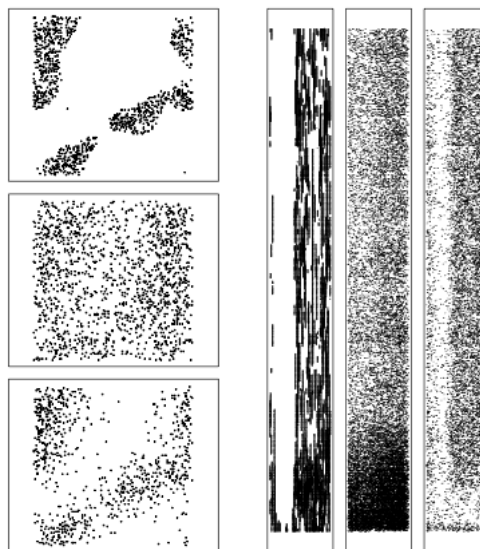
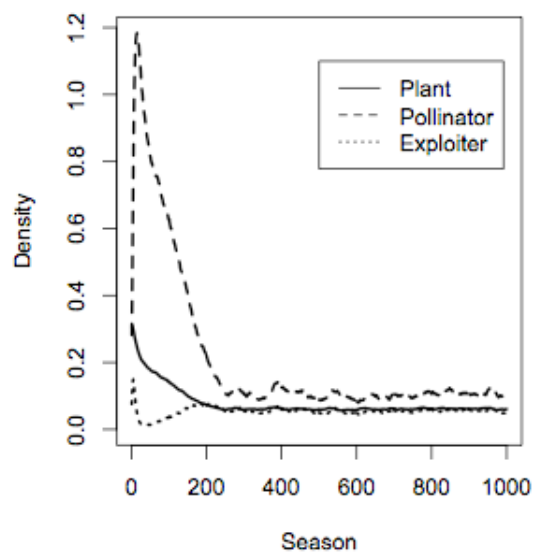
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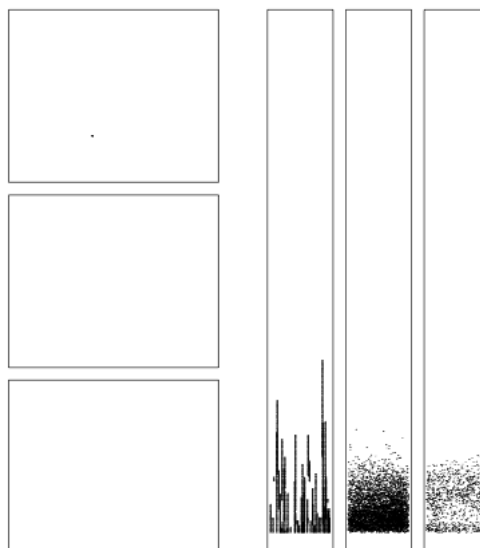
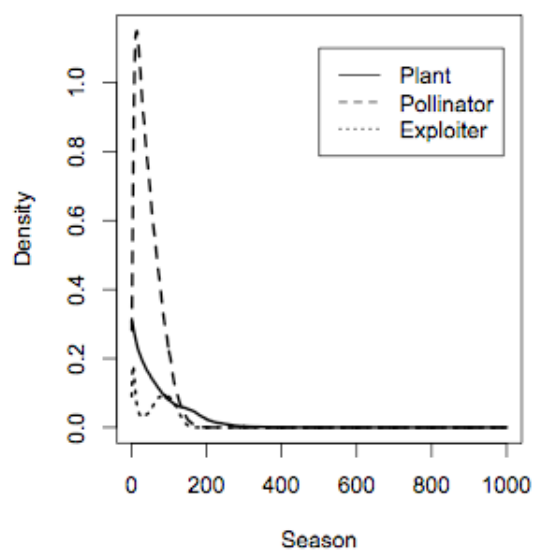
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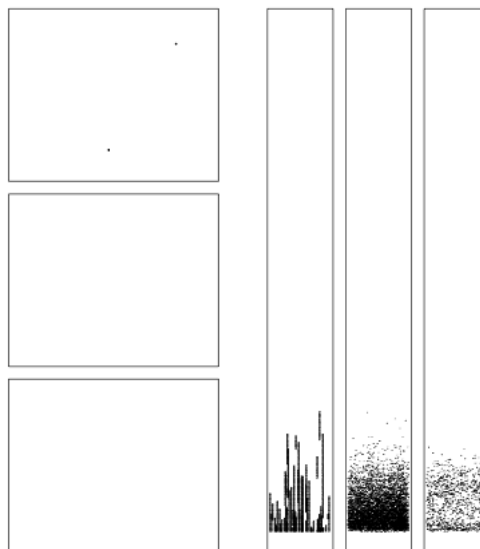
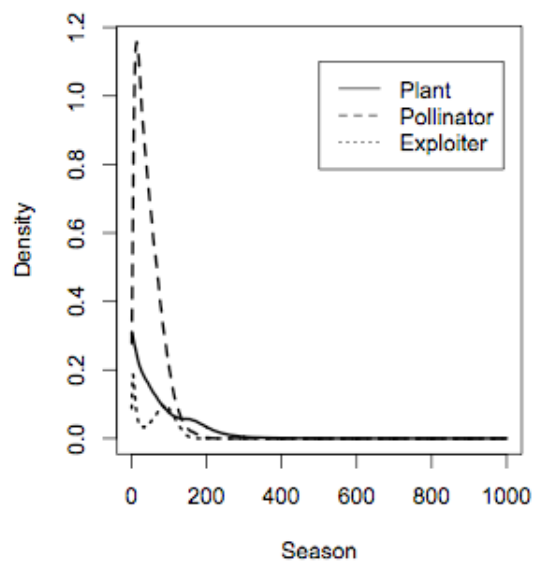
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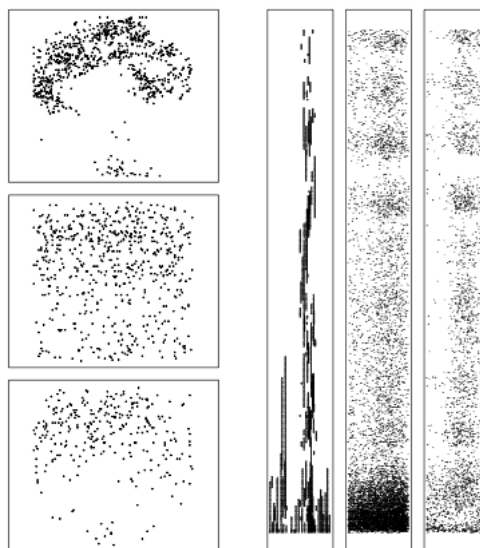
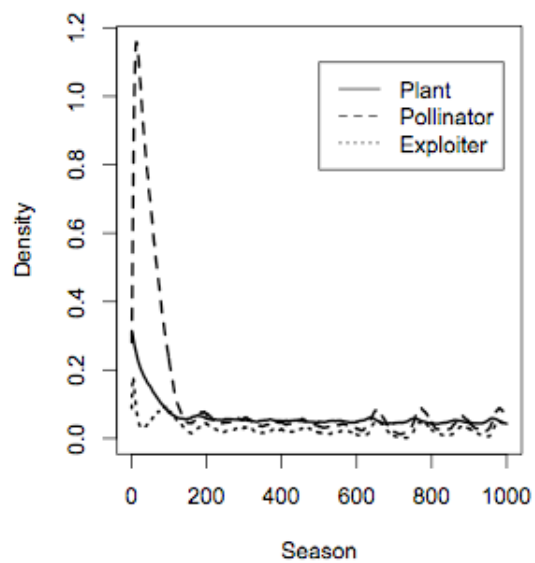
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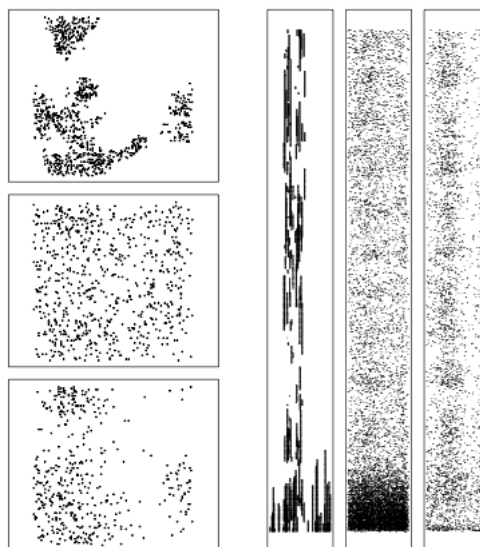
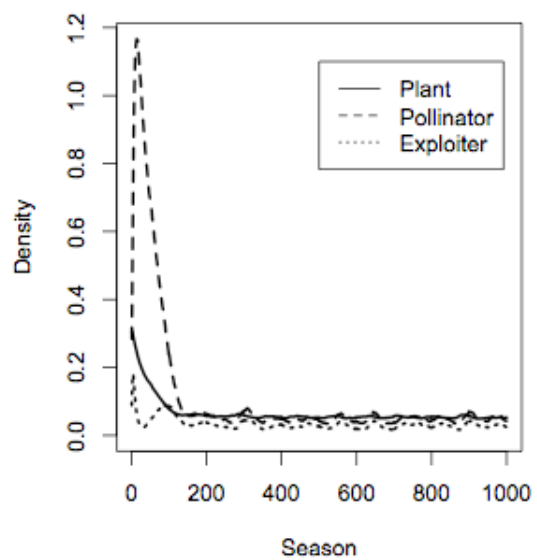
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$$\Delta_P = 10 ; \Delta_M = 10; \Delta_E = 2; \epsilon = 25 ; \beta = 2$$



$$\Delta_P = 10 ; \Delta_M = 10; \Delta_E = 2; \epsilon = 25 ; \beta = 3$$



6 9. Supplemental Information 2

The 100 replicate simulations resulted in means with very low standard errors for all parameter combinations used. Error bars showing a 95% range around each point would not be clearly distinguishable from the points in the figures. To give an idea of the consistency of our results for a particular parameter combination, below is the mean number of pollinator visits per flower, \pm the standard error, for each level of habitat autocorrelation at default parameters of our model.

Further, our intention in this model is to better understand the mechanisms affecting mutualism properties and community coexistence. Because these mechanisms are directly observed in modeling – we use figures to facilitate the understanding of these mechanisms, and to summarize. We are not interested in whether or not the difference between particular simulations (e.g., pollinator visitation at long vs. short range pollinator dispersal at some specified level of habitat autocorrelation) are statistically significant per se.

Autocorrelation (β)	Pollinator Visitation
0.0	3.482073 \pm 0.009794566
0.5	3.671846 \pm 0.008705665
1.0	3.982356 \pm 0.009467323
1.5	4.562163 \pm 0.012891480
2.0	5.226168 \pm 0.016397787
2.5	5.875864 \pm 0.019603746
3.0	6.318901 \pm 0.020116723
3.5	6.575353 \pm 0.021329411
4.0	6.748689 \pm 0.016403742
4.5	6.818482 \pm 0.017844348
5.0	6.878280 \pm 0.017524008
5.5	6.902440 \pm 0.016761871
6.0	6.901064 \pm 0.016835329

CHAPTER III. THE EFFECTS OF DENSITY ON MUTUALISM COSTS AND BENEFITS: AN EMPIRICAL TEST WITH FIGS AND FIG WASPS

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A manuscript to be submitted to the *Journal of Biogeography*

Abstract

Aim

To determine how the aggregation of host plants affects the costs and benefits of inter-specific interactions with insect mutualists (pollinators) and antagonists (herbivores). We test recent theory by investigating four hypotheses using *Ficus petiolaris* and its associated pollinating and non-pollinating (galling) wasps: 1) The number of pollinating wasps visiting receptive fig fruits will increase with increasing local fig tree density, and 2) the number of pollinator offspring produced within mature fig fruits will increase with pollinator visitation, while 3) the number of seeds and 4) the number of non-pollinating exploiters of the mutualism will decrease with increasing local fig tree density.

Location

Six *F. petiolaris* populations along a latitudinal gradient in Baja California, Mexico.

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Methods

We estimate the density of *F. petiolaris* in the vicinity of sampled trees by counting the number of neighboring reproductive-size conspecifics over three orders of magnitude (0.1-15 km). We sample 700+ ripe fig fruit from 65 independent fig crops over a five-year period. We count the number of arriving foundress pollinators, pollinator offspring, seeds, and non-pollinators within fig fruits, then regress counts against the number of neighboring conspecific figs.

Results

For spatial scales of neighboring conspecific fig trees within the reported dispersal range of pollinators (5-15 km), we found foundress counts to significantly increase with neighboring fig density, and pollinator production to significantly increase with foundress counts. We further found seed and non-pollinator counts to significantly decrease with neighboring fig density and foundress counts.

Main conclusions

We find our hypotheses to be strongly supported. We conclude that the aggregation of plants can strongly influence the costs and benefits of interspecific interactions between mutualists and antagonists. We additionally conclude that the aggregation of pollinators and non-pollinating exploiters may play a key role in stabilizing plant-pollinator-exploiter systems.

Introduction

Mutualisms are defined by interactions between species that are reciprocally beneficial. Such interactions are ubiquitous in nature (Janzen, 1985; Bronstein, 2001*a*), making their study of critical importance to the understanding of ecological and evolutionary processes. In addition to conferring fitness benefits to symbionts, the ecology and evo-

lution of mutualism includes diverse costs (Bronstein, 2001*a*; Morris et al., 2010). Such costs are incurred in the production of goods and the provision of services exchanged for beneficial resources. The costs and benefits involved in mutualistic interactions are not always easily quantified. Much has been learned from plants associated with obligate seed-eating pollinators, however, because in such systems costs and benefits are easily measured in terms of the numbers of seeds and pollinators that plants produce. The fitness gain accrued by the production of seeds and pollinators is different for each mutualist partner. Plants benefit from the production of both seeds and new pollinators, which represent plant female and male fitness, respectively, while pollinators do not benefit from the production of seeds. Because asymmetry in fitness interest is expected for all mutualisms (Herre et al., 1999), studies of plants and their seed-eating pollinators are of broad conceptual interest. Further, several characteristics of these interactions make them especially useful for theoretical and empirical research. Theoretical modeling is facilitated by the discrete nature of costs and benefits (Morris et al., 2010), and by the direct way in which pollinator and seed production affect population dynamics (e.g., Bronstein et al., 2003; Morris et al., 2003; Wilson et al., 2003) and individual fitness (e.g., Jones et al., 2009). Empirical studies are facilitated by the tractability of estimating seed and pollinator production from dissected plant tissue, and of comparing across mutualisms (Bronstein, 2001*a*).

Given their useful characteristics, it is unsurprising that some of the best known examples of mutualism include highly co-evolved systems of interacting plants and seed-eating pollinators such as figs and their pollinating wasps (e.g., Janzen, 1979*a*; Bronstein, 1988; Herre and West, 1997; Weiblen, 2002; Herre et al., 2008) and yuccas and their pollinating moths (e.g., Keeley et al., 1984; Addicott, 1986; Keeley et al., 1986; Pellmyr and Huth, 1994; Pellmyr, 2003). Other seed-eating mutualisms include the interactions between senita cacti and their pollinating moths (e.g., Holland and Fleming, 1999), globe-

flowers and their pollinating flies (e.g., Després and Jaeger, 1999; Després et al., 2007), and Phyllanthaceae (Phyllanthaceae) plants and their pollinating moths (e.g., Kato et al., 2003; Kawakita, 2010). Empirical studies of all these mutualisms observe that the costs incurred and benefits obtained by plants in terms of pollinator and seed production can vary greatly. For example, in a study including 23 Florida strangling figs (*Ficus aurea*), Bronstein (2001a) found pollinator production within fig fruit (technically syconia – enclosed inflorescences) to range between 0-229, and seed production to range between 0-150. Such variation among figs within a population is typical, with high variation in pollinator and seed production reported for species in South and Central America (e.g., Janzen, 1979b; West and Herre, 1994; West et al., 1996; Bronstein and Hossaert-McKey, 1996; Cardona et al., 2012), Africa (e.g., Compton and Nefdt, 1989; Nefdt and Compton, 1996), Australia (e.g., Cook and Power, 1996), and Asia (e.g., Wang et al., 2005a,b; Yu and Compton, 2012). Multiple studies have likewise found high variation in among plant seed and pollinator production in yuccas (e.g., Keeley et al., 1984; Addicott, 1986), senita cacti (e.g., Holland and Fleming, 1999), globeflowers (e.g., Jaeger et al., 2001; Després et al., 2007), and *Glochidion* plants (e.g., Kato et al., 2003). To comprehensively understand mutualism, it is necessary to also understand the causes of this high variation in mutualism costs and benefits.

The production of pollinators and seeds in plants with seed-eating pollinators is likely to be strongly influenced by pollinator density, which will directly affect the frequency of pollinator visitation to plants. Plants that are visited by more pollinators when receptive for pollination may be more effectively pollinated (e.g., Després et al., 2007), but will also have increased levels of seed predation from pollinator larvae (e.g., Herre, 1989; Pellmyr, 1989; Holland and DeAngelis, 2002; Shapiro and Addicott, 2003). As a result, mutualism costs and benefits for plants with seed-eating pollinators will be strongly affected by the number of visiting pollinators. The number of pollinators visiting a plant may likewise

affect pollinator fitness. For example, the per capita production of pollinator larvae decreases with the number of fig-wasp foundresses entering fig syconia (Herre, 1989). And the probability of fruit abortion (and thus pollinator larval mortality) in yuccas increases with seed predation from moth pollinators (Pellmyr and Huth, 1994; Richter and Weis, 1995). Even in the absence of fruit abortion, provided that the populations of both mutualists are sufficiently dense to avoid Allee effects (Holland and DeAngelis, 2001; Morris et al., 2003; Gates and Nason, 2012), negative density-dependent feedback will prevent pollinator visitation from reaching levels in which the overexploitation of plant resources leads to the extinction of both mutualists. When pollinator density becomes too high, plant seed production decreases, resulting in lowered plant density and a subsequent decrease in pollinator population growth that ultimately leads to stable populations or dampened oscillations in ecological models (Holland et al., 2002; Morris et al., 2003; Wilson et al., 2003).

Given the density-dependent regulation predicted by ecological models, the high variation observed among plants in seed and pollinator production may suggest that density-dependent mechanisms are weak in regulating plant and seed-eating pollinator interactions (Addicott, 1986). Alternatively, spatial variation in pollinator densities may lead to variation in pollinator and seed production with populations still regulated strongly by density-dependent mechanisms. In population models, the densities of plants and their seed-eating pollinators are implicitly assumed to have a uniform effect on individuals of both mutualists, with a decline in pollinator density decreasing pollinator visitation equally for all plants. Individual-based models allow for variation in a population, including variation in the local density of individuals through the modeling of explicit space. In a spatially explicit model of plants and seed-eating obligate pollinators, Duthie and Falcy (2013) vary the aggregation of plants by varying plant habitat autocorrelation. When the spatial distribution of plants is aggregated, and the dispersal of pollinators is limited,

the mean number of pollinator visits a plant receives will be strongly influenced by the plant's location. Areas of habitat in which plants are closely aggregated will be visited more frequently by pollinators, increasing pollinator production at the cost of seeds. In contrast, areas where plants are more spatially isolated will be visited less frequently by pollinators, which may increase seed production but also decrease the probability of pollen transfer. Additionally, plants that are more geographically isolated may have an increased risk of being exploited by species that eat seeds but do not pollinate (Duthie and Falcy, 2013).

Mutualisms are almost universally exploited by individuals that obtain resources or services without incurring the costs associated with providing resources or services in return (Bronstein, 2001*b*). By far the most common types of exploiters are specialist species associated with mutualists. Obligately exploiting species are especially diverse in the interactions between figs and their pollinating wasps. While most of the 750+ described species of figs are each pollinated by a single host-specific wasp species, they are additionally associated with a diverse community of non-pollinators that oviposit within fig syconia. Non-pollinator wasps are typically host-fig-specific (Weiblen, 2002), and each species of fig typically includes 2-30 non-pollinating species (Compton and Hawkins, 1992). Many of these non-pollinator species are obligate exploiters of the mutualism, though some are parasitoids or inquiline predators.

Theoretical studies of plants and their seed-eating pollinators have modeled the ecological (e.g., Bronstein et al., 2003; Morris et al., 2003; Wilson et al., 2003; Duthie and Falcy, 2013) and evolutionary (e.g., Ferrière et al., 2002, 2007; Jones et al., 2009) consequences of exploitation. Unlike the the case of pairwise interactions between plants and seed-eating pollinators, sufficient densities of both mutualists does not guarantee species coexistence when exploiters are present. The presence of exploiters can lead to one of three outcomes depending on relative exploiter birth rate (Morris et al., 2003).

When exploiter birth rate is too low, exploiters are competitively excluded by pollinators. At very high levels of exploiter birth rate, both mutualists (and exploiters in turn) are driven to extinction. Only at intermediate birth rates are exploiters predicted to coexist with mutualists, but the inclusion of spatial structure is highly stabilizing in models of plant-pollinator-exploiter interactions (Wilson et al., 2003). Further, when plant habitat is spatially heterogeneous, the spatial distribution of plants can sometimes affect community dynamics strongly enough to lead to any coexistence outcome given the same set of demographic parameters (Duthie and Falcy, 2013). When plants are strongly autocorrelated on a landscape, the frequency at which they are visited by pollinators increases leading to a higher pollinator birth rate and increased likelihood of exploiter exclusion. As plant autocorrelation decreases, so does pollinator birth rate, leading to increased exploitation. Spatially, the model of Duthie and Falcy (2013) predicts exploiter production to be highest in areas where plants are remote, and lowest where plants are especially dense. Such spatial aggregation of pollinators and exploiters may affect intraspecific competition and have evolutionary consequences. Theory suggests that weak competition among conspecific mutualists can lead to the evolutionary purging of exploiters, and weak competition among conspecific exploiters can lead to evolutionary suicide for the entire community (Jones et al., 2009).

Here we test the predictions of Duthie and Falcy (2013) using a natural community that includes a fig, its species-specific pollinator mutualist, and a guild of host-fig-specific non-pollinating exploiters. Using the explicit spatial locations of *F. petiolaris* trees from multiple populations in Baja California, as well as counts of pollinator foundresses, pollinator offspring, seeds, and non-pollinator offspring from mature fig fruits (technically and hereafter syconia), we test four specific hypotheses: 1) The number of foundresses arriving at fig syconia increases with the density of neighboring fig trees, 2) pollinator production will increase with the number of arriving foundresses, 3) the number of seeds

produced by fig syconia will decrease with the density of neighboring fig trees, and 4) the number of non-pollinator larvae produced by fig syconia will decrease with the density of neighboring fig trees.

Methods

The Sonoran Desert rock fig, *F. petiolaris* (family Moraceae, subgenus *Urostigma*, section *Americana*), is endemic to the Sonoran Desert of Baja California and adjacent mainland Mexico. Like all monoecious figs, *F. petiolaris* trees produce enclosed inflorescences (syconia) that contain multiple flowers. These flowers line the inner cavity of the syconia with styles of varying length pointing toward the interior. Flower production per syconia in *F. petiolaris* can range between roughly 150-700 depending on syconia size. Although most fig species produce syconia in synchronous bouts that can be separated by periods of several months to years (Bronstein, 1989; Windsor et al., 1989), nearly half of *F. petiolaris* trees produce syconia with at least some degree of within-crown asynchrony (Gates and Nason, 2012). Asynchronous reproduction allows for greater overlap in phenology among trees when population densities are low, as is common in *F. petiolaris* (Gates and Nason, 2012). Here we sample only from trees located in Baja California, where *F. petiolaris* is the sole endemic species of fig.

F. petiolaris is pollinated by a single and unnamed specialist species of *Pegoscapus* wasp (superfamily Chalcidoidea, family Agaonidae). Mated, pollen bearing “foundresses” are attracted to volatile cues released by trees when syconia are in “female phase,” and contain female flowers that are available for pollination and pollinator oviposition (van Noort et al., 1989; Ware and Compton, 1994a,b; Grison-Pigé et al., 2002). Upon arrival, foundresses enter syconia through a small bract-lined opening, then actively pollinate female flowers while ovipositing their eggs into a subset of fig ovules. After pollination and oviposition, syconia enter into “interphase,” a period in which pollinator wasps and seeds develop over several weeks. After development is complete, syconia enter into “male

phase,” and male pollinators chew their way out of ovules and compete for access to mate with females, which lack the ability to exit ovules on their own and are often full siblings. After mating, females collect pollen, then exit syconia through holes drilled by males to disperse to new receptive trees. Seeds that remain in syconia are often dispersed by various species of frugivores.

The community of non-pollinating fig wasps associated with *F. petiolaris* includes seven species, all of which oviposit into fig syconia externally by inserting their ovipositors through syconia walls. Each species of non-pollinator is regularly found in all fig populations, often developing within the same syconia. The community includes three species of *Idarnes* and two species of *Heterandrium*, all of which gall fig ovules like pollinators. The community also includes a species of *Aepocerus*, which produces especially large galls that protrude into the center of syconia and appear to originate from the tissue of the syconium wall. *Aepocerus* is parasitized by a specialist species of *Physothorax*.

Trees of *F. petiolaris* were mapped for six populations along a latitudinal gradient on the Baja California peninsula (Figure 1; Site 70, Lat. = 23.73769, Lon. = -109.82887; Site 96, 24.03380, -110.12570; Site 113, 27.14852, -112.43554; Site 112, 27.55689, -113.05923; Site 172, 28.29069, -113.11197; Site 158, 29.2627, -114.02090). Between 2005-2010, 723 male phase syconia from 65 crops representing 61 unique trees were collected, partially cut open, and placed in individual vials overnight (min 12 hrs) to allow sufficient time for wasp larvae to emerge. Emerged wasps were preserved in 95% ethanol, then shipped to Iowa State University where counts of pollinators, seeds, and non-pollinators were obtained for individual syconia. Because foundress *Pegoscapus* wasps nearly always die within the syconia in which they pollinate and oviposit (Herre, 1989), and foundress corpses typically remain intact inside syconia through male phase, we were able to obtain estimates of arriving foundress number for 624 syconia from 43 trees. To estimate seed counts, syconia were dried, and seeds were placed in separate

coin envelopes and shipped to Iowa State University. Seed counts were available for 210 syconia from 21 trees.

To estimate the density of neighboring fig trees, for each tree from which syconia were sampled, we defined neighbors as any trees within a Euclidean distance of r . To ensure that our results were not scale dependent, we used six r values spanning over three orders of magnitude, including $r = 0.1$ km, 0.5 km, 1.0 km, 5.0 km, 10.0 km, and 15.0 km. A number of neighbors was determined for each r value for all sampled trees. To test whether or not the number of neighboring fig trees was positively correlated with foundress counts, we used R (R Development Core Team, 2011) to fit six separate linear regression models using foundresses per syconium as a dependent variable and counts of neighbor trees for each r as an independent variable. The same analysis was performed using pollinator, seed, and non-pollinator counts per syconium as dependent variables to test whether or not pollinator, seed, and non-pollinator production decreased with neighboring tree density, respectively. In the case of non-pollinators, only exploiter wasps were used in the analysis, which included all species except the parasitoid *Physothorax*.

When regressing pollinator, seed, and non-pollinator counts against the number of neighboring figs, foundress counts were included as an additional independent variable in the linear models. Although it is well-established that foundress counts are expected to be positively correlated with pollinator counts (e.g., Herre, 1989; West and Herre, 1994; West et al., 1996), we regressed pollinator counts against foundress counts to confirm this relationship. Because all of the dependent variables were Poisson distributed (Figure 2), a Poisson error structure was used in all regressions. In all regressions, data were overdispersed (the variance was greater than the mean), so an empirical scale parameter was applied to account for the overdispersion (Crawley, 2005).

Results

The results showing the impact of neighboring fig density on foundress counts, pollinator production, seed production, and exploiter production are shown in Tables 1-4. Foundress counts increased significantly with the number of neighboring trees when neighbors were defined to be within 5-15 km, but this increase was not significant when neighbors were defined to be within 0.1-1 km (Table 1). Foundress count significantly increased the production of pollinators (Figure 3) at all neighbor scales, and the effect of fig tree density by itself was never significant for pollinator production (Table 2). The number of seeds produced by syconia decreased with increasing numbers of neighboring trees when neighbors were defined to be within 5-15 km, but this decrease was also not significant when neighbors were defined to be within 0.1-1 km (Table 3). At all scales for which neighbors were defined, exploiter production decreased with increasing neighbor density (Table 4).

Seed production significantly increased with the number of arriving foundresses at the 0.1 km scale, but significantly decreased with foundress counts at scales of 10-15 km (Table 3). At the 0.1 km scale, we found a significant negative interaction between neighboring fig density and foundress count, suggesting that when the number of arriving foundresses was higher, seed production decreased even more with higher neighbor density. The contradictory result at scales of 10-15 km was the only case in which we observed a different and significant effect at differently defined r values. At scales of 10-15 km, the interaction between neighboring fig density and foundress counts was significantly positive (Table 3). In biological terms, the effect of neighbor density and foundress counts on seed production was negative, but the effect of neighbor density was less negative when foundress counts were high.

At all scales at which neighbors were defined, the number of exploiters within syconia significantly decreased with increasing foundress counts. The interaction between neigh-

bor density and foundress count was significantly positive at neighbor scales of 0.1-5.0 km, but not for scales of 10-15 km. Thus, while neighbor density and foundress count have negative effects on exploiter production, neighbor density has less of a negative effect when foundress counts are high.

Although the impact of neighbor density on foundress counts was highly significant at scales of 5-15 km, neighbor density only explained 2-3% of foundress count variation (Table 1). At these same scales, neighbor density explained 7-9% of the variation in seed production (Table 3), and 1-2% of the variation in production of exploiters (Table 4). At scales of 0.1-1.0 km, however, neighbor density explained up to 10% of the variation in exploiter production. The amount of variation explained by foundress counts was similarly low, with 3-7% and 2-6% explained for seed and exploiter production, respectively.

Discussion

The syconia of fig trees are ephemeral resources for both pollinating and non-pollinating fig wasps. Although some fig species, including *F. petiolaris* (Gates and Nason, 2012), regularly fruit asynchronously (e.g., Bronstein and Patel, 1992; Cook and Power, 1996), the production of syconia is never continuous. Fig wasps must routinely search for new fig trees with receptive syconia, which may be located far from their natal trees (Nason et al., 1998; Ahmed et al., 2009). This is likely to lead to both high and highly variable dispersal mortality, which will be affected by the location and timing of syconia development in conspecific fig trees. As a result, much variation in pollinator, seed, and exploiter production will likely depend on the stochastically varying accessibility of receptive fig syconia to wasps. Despite this high predicted stochasticity, we found that the spatial aggregation of fig trees significantly increased the number of foundresses arriving to syconia, which in turn significantly increased pollinator production. We also found fig tree aggregation to significantly decrease seed and exploiter production, as predicted by

theory (Duthie and Falcy, 2013).

It is well established that the spatial distribution of individuals among and within populations can have a strong impact on species interactions. For example, among populations, the strength or even nature of species interactions can be modified by additional species. This is the case for the herbaceous plant *Lithophragma parviflorum* and its mutualist and seed eating pollinator *Greya politella* (Thompson and Cunningham, 2002). Unlike the highly specialized plant-pollinator interaction between figs and their pollinating wasps, in some habitats *L. parviflorum* is pollinated by additional co-pollinators that do not feed on developing flowers as larvae. In habitats in which *G. politella* is the exclusive pollinator of *L. parviflorum*, the plant-pollinator relationship is mutualistic. But where co-pollinators occur, and *L. parviflorum* is not reliant on *G. politella*, the interaction can be commensal or antagonistic (Thompson and Cunningham, 2002; Thompson and Fernandez, 2006). On a smaller scale, within populations, species interactions can be affected by the spatial arrangement of one or more species. This is the case for plants that engage in symbiotic interactions with ant colonies, such as the flowering *Cordia nodosa*, which is endemic to the tropical understory forests of South America (Davidson and McKey, 1993). Ants colonies that reside within individual *C. nodosa* plants offer protection from herbivory, but the net impact of the ant symbiosis differs depending on the genus of the symbiotic ant colony. Interactions between *C. nodosa* and *Azteca* ants are mutualistic, but *Allomerus* ants are unique in castrating their hosts by destroying flowers and inhibiting fruit development; this behavior increases host growth and ant colony fecundity (Yu et al., 2004). Thus, *Allomerus* ants are both antagonistic to the mutualism and more fecund than the mutualistic *Azteca* colonies. The coexistence of *Allomerus*, *Azteca*, and their *C. nodosa* hosts relies on a competition-colonization trade-off between ant genera. While *Allomerus* colonies are more fecund, *Azteca* ants are superior colonizers of *C. nodosa* hosts (Yu and Wilson, 2001). This competition-colonization

trade-off leads to community dynamics that are dependent upon the spatial arrangement of *C. nodosa* plants. In habitats wherein plant density is high, the antagonistic *Allomerus* ants dominate, but where plant are more sparse, *Azteca* ants are competitively superior.

For plants, their seed-eating pollinators, and associated exploiters, theory predicts the distribution of plant habitat to be influential to the costs and benefits associated with mutualisms (Duthie and Falcy, 2013). Where plant habitat is positively autocorrelated, plants are expected to also be spatially aggregated. Where plants are aggregated, they are expected to be visited more frequently by seed-eating pollinators, which are produced in the nearby developing flowers of conspecific plants. More isolated plants, in contrast, will likely be visited by fewer pollinators because fewer nearby conspecifics are available to supply these pollinators. As a result, the costs and benefits associated with the mutualism are expected to vary spatially in a predictable way. Where conspecific plants are aggregated, more flowers will be used for pollinator production due to a higher number of arriving pollinators, leaving fewer flowers left to produce seeds. But because pollinators in seed-eating mutualisms are often competitively superior to exploiters, either because pollinators preempt exploiters in oviposition or are required to prevent fruit abortion, where conspecific plants are aggregated they are also expected to have fewer flowers lost to exploitation. In this study, we tested whether or not pollinator visitation to fig trees increased with the density of neighboring fig trees at multiple spatial scales, resulting in higher pollinator production and lower seed and exploiter production. When neighboring fig trees were defined to include conspecifics at broad scales (5-15 km), we found our predictions to be strongly supported.

The scale at which spatial processes are expected to be ecologically relevant to interacting species will be strongly influenced by the dispersal habits of individuals within a community. MacArthur (1972) described habitats as hierarchically structured, with complex sub-habitats that vary at finer geographic levels. The distance over which indi-

viduals regularly disperse will determine the turnover of habitat heterogeneity in species interactions. Individuals that disperse relatively short distances will be affected by environmental changes at finer geographic scales. In contrast, individuals that disperse relatively long distances will experience habitat turnover at broader geographic scales. As such, interpreting our results requires some consideration of the dispersal capabilities of mutualists and exploiters, especially the dispersal capabilities of pollinating and non-pollinating fig wasps, which we predicted to vary spatially as a function of plant density. Ideally, relevant spatial scales would be determined by data collected from careful observations of wasp dispersal behavior, but because of the small size of pollinating and non-pollinating fig wasps, such observations are impractical. Genetic analyses of figs native to central Panama, however, show that pollinating fig wasps of the genus *Pegoscapus* routinely transfer pollen between 5.8-14.2 km (Nason et al., 1998). As such, it is unsurprising that the hypotheses of Duthie and Falcy (2013) were supported most strongly at the 5.0-15.0 km scales. It would be interesting to test whether or not these predicted patterns are observed at much broader spatial scales, but practical limitations to fig censuses in the field restricted our ability to estimate fig neighbor densities with confidence across broader geographic distances.

The significant decrease in exploiter production with neighboring fig density at scales <5.0 km (Table 4) suggests that exploiters as a group are more dispersal limited than pollinators. This conclusion appears to be supported by preliminary genetic analyses of the exploiters of *F. petiolaris* (J. Nason, unpublished data), but to our knowledge, no study exists comparing the relative dispersal abilities of pollinating and non-pollinating fig wasps. Consistent with the mechanism predicted by Duthie and Falcy (2013), exploiter production decreased with the number of foundresses at all scales at which neighbors were defined (Table 4). This decrease in exploiter production is likely caused by foundresses preempting exploiters in ovipositing into developing flowers. High numbers

of foundresses will result in more flowers used for pollinator production (Table 4), but may also reflect oviposition timing effects. Syconia with higher numbers of foundresses were likely pollinated and used for oviposition earlier in development than syconia with fewer foundresses, leaving less time for exploiters to oviposit. At 0.1-5.0 km scales, we found a positive interaction term between neighbor density and foundress count impacting exploiters, suggesting that neighbor density decreases exploiter production less when foundress counts are high. One plausible explanation for this observation is that areas of especially high fig neighbor density are correlated with relatively low exploiter density, as predicted by theory (Duthie and Falcy, 2013). Thus fewer ovipositing exploiters are present in these areas to be affected by the preemption of flowers by ovipositing foundresses. This interpretation is also consistent with the positive interaction between neighbor density and foundress count observed to affect fig seed production at scales >5 km. If fewer exploiters are in the area to oviposit, fewer pollinated flowers that would otherwise become seeds will be lost to exploiter production.

The spatial aggregation of pollinators and non-pollinating exploiters may have broad implications for the ecology and evolution of fig-fig wasp mutualisms and related systems. For some fig species, the aggregation of foundresses where fig trees are most dense may lead to an increase in intraspecific competition among pollinators in these regions. Because the per capita production of pollinators can dramatically decline with increasing numbers of arriving foundresses (Herre, 1989), wasp fitness may be decreased in areas where fig trees are especially dense. If the reduction in pollinating fig wasp fitness due to competition is strong enough where fig trees aggregate, selection might be expected to favor pollinators capable of avoiding especially dense regions of figs. Indeed, within the crowns of receptive fig trees, the distributions of some foundresses have been observed to be overdispersed with respect to syconia, suggesting that foundresses can avoid syconia that have been previously entered by other pollinators (Ware and Compton, 1994*b*). It

is tempting to suggest that the fitness benefits of avoidance behavior at the scale of fig crowns could select for long distance dispersal, with wasps capable of reaching more remote fig trees receiving a fitness benefit by avoiding competition. While this might be an interesting hypothesis, it is unlikely to be compatible with the the extreme dispersal capabilities and behaviors of pollinating fig wasps. Dispersal of pollinators is largely wind-borne (Ware and Compton, 1994*a,b*), with pollinators attracted to volatile compounds produced by receptive figs (van Noort et al., 1989; Ware and Compton, 1994*a,b*; Grison-Pigé et al., 2002). When pollinators recognize volatile cues, they must rapidly lose altitude to avoid winds and direct their flight toward receptive syconia. Given the extent to which wasp dispersal is directed by wind, and that a high proportion of pollinators are likely to be unsuccessful dispersers, it is unlikely that pollinators are able to discriminate among receptive fig crowns. Further, pollinators of ecologically similar mutualisms are known to disperse much more modest distances (e.g., Marr et al., 2000). As such, while foundresses may receive a short term fitness benefit from successfully dispersing to receptive fig trees with relatively few conspecific neighbors, this benefit is not a plausible evolutionary explanation for the extremely long range dispersal capabilities of fig wasps (Nason et al., 1998; Ahmed et al., 2009).

More plausible consequences of pollinator and exploiter spatial aggregation include those that are likely to affect the long term ecological and evolutionary stability of the plant-pollinator mutualism. Because nearby wasps are expected to compete directly for access to developing flowers, pollinator and exploiter spatial aggregation is expected to result in higher intraspecific competition for pollinators and exploiters. Morris et al. (2003) modeled the impact of intraspecific competition on community dynamics and coexistence in seed-eating mutualisms that include a species of exploiter. They found increasing intraspecific competition for both pollinators and exploiters to greatly widen the range of demographic parameters over which stable coexistence occurs, even given

the competitive superiority of pollinators (Morris et al., 2003). The spatial aggregation of pollinators and exploiters may thus play a role in facilitating coexistence through intraspecific competition. Additionally, regions wherein fig trees are sparser and visited less frequently by foundresses may be especially influential in maintaining populations of exploiters. Our results showing an increase in exploiter production where fig trees have fewer nearby conspecifics are comparable to those of Wang et al. (2005a), who examined the production of pollinating and non-pollinating fig wasps associated with *F. racemosa* in primary forest, fragmented forest, and highly fragmented forest in Xishuangbanna, Yunnan, China. They observed the proportion of non-pollinating wasps to be significantly higher in highly fragmented forest habitat than in primary forest habitat.

In addition to affecting species population dynamics and coexistence, increased exploitation from non-pollinators in regions where figs trees are sparse may have long-term consequences for the evolutionary stability of the fig-fig wasp mutualism. In mutualism, theory predicts competitive asymmetry between mutualists and exploiters to be important to evolutionary stability (Ferrière et al., 2002). When mutualists are not competitively superior to exploiters, selection is expected to reduce the amount of goods or services provided by mutualists to their partners, ultimately driving the mutualism to extinction. Thus, even if mutualist communities that include exploiters are ecologically stable, the long term evolutionary persistence of these communities is not guaranteed (Ferrière et al., 2002, 2007; Jones et al., 2009). Jones et al. (2009) examined the role of mutualist and exploiter intraspecific competition in long term mutualism evolutionary stability. They found increased intraspecific competition of mutualists and exploiters to be highly stabilizing, leading to coevolutionary stable equilibriums that result in the coexistence of all species. Among competitors, intraspecific competition is expected to be increased when species aggregate spatially near limiting resources. The spatial aggregation of pollinators and exploiters observed here and in other fig wasp associations

(e.g., Wang et al., 2005a) therefore predicts increased intraspecific competition, and may contribute to the coevolutionary stability of the fig-fig wasp mutualism, and mutualisms that include exploiters more generally.

Understanding the spatial processes that facilitate the ecological and evolutionary coexistence of figs and their associated pollinating and non-pollinating wasps is not only interesting within the scope of evolutionary ecology, but also for species conservation. When food is scarce, tropical figs provide a keystone resource for a diversity of frugivores year round (e.g., Leighton and Leighton, 1983; Terborgh, 1986; Lambert and Marshall, 1991; Korine et al., 2000). Given the importance of fig resources to frugivores, the production of pollinators and seeds may have far reaching implications for patterns of biodiversity in regions where species are limited by fig density. Such regions may include communities incurring habitat fragmentation in areas of human disturbance, where figs have been suggested to be an increasingly vital source of food for frugivores when other resources are scarce due to habitat loss (Bronstein and Hoffmann, 1987). As the importance of figs as a keystone resource increases, however, fragmentation may shift the ecological and evolutionary dynamics between mutualists and exploiters. High fragmentation may lead to low densities of fig trees, and increase the birthrate of non-pollinating exploiters (Wang et al., 2005a), a prediction supported by our results for *F. petiolaris*. Given sufficiently low tree density, this fragmentation alone may be sufficient to threaten the stability of fig-fig wasp mutualisms by lowering pollinator visitation and increasing exploitation (Duthie and Falcy, 2013).

Our results may also have broad implications for the ability of plants associated with seed-eating pollinators to adapt to new habitats, especially at the margins of plant ranges. Areas in which plants are especially dense are expected to be areas that are also high quality habitat. If high habitat quality leads to both high local plant density and, in turn, disproportionately high pollinator production, then plant populations will

be gender dimorphic, with plants in higher habitat quality being functionally more male than plants in lower habitat quality. At the landscape level, aggregated plants in high quality habitats will be net exporters of pollinators, and more sparsely distributed plants in lower quality habitats will be net exporters of seeds. Depending on the degree to which pollen versus seed dispersal contribute to total gene flow, the genetic structure of plants may be dominated by gene flow from high density locals (if pollen contributes more total gene flow) or from more sparsely distributed plants in less high quality habitats (if seeds contribute more total gene flow). For most plants, pollen flow is typically over an order of magnitude higher than seed flow (Petit et al., 2005). Figs appear to be no exception; genetic evidence suggests that pollen transfer contributes more strongly to gene flow than seed dispersal among fig populations (Yu et al., 2010; Yu and Nason, 2013). In a study of *F. hirta*, the ratio of pollen to seed migration was observed to be 16.2-36.3 (Yu et al., 2010). Given the dominance of gene flow from pollen transfer, the genetic structure of fig populations is likely to be influenced disproportionately by trees in aggregated patches where habitat quality is high. Such disproportionate gene flow from areas of high habitat quality to low habitat quality may erode the influence of natural selection on local adaptation, limiting adaptation to novel environments at the margins of fig ranges (Kirkpatrick and Barton, 1997; Gaston, 2009).

In conclusion, we find predictions of Duthie and Falcy (2013) to be strongly supported by data collected from *F. petiolaris* and its associated fig wasps. When conspecific fig trees are aggregated, syconia receive higher numbers of foundresses to pollinate and oviposit into flowers. More foundresses result in a higher proportion of flowers used for developing pollinators than seeds. Where trees are relatively isolated, fewer foundresses arrive in syconia, leading to increased exploitation of the mutualism, but also higher seed production. Our results show that spatial variation in the density of plants that rely on seed-eating pollinators can play an important role in species interactions and influence

the costs and benefits associated with mutualisms.

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Scale at which neighbors defined (<i>r</i>)						
Ind. Variable	0.1 km	0.5 km	1.0 km	5.0 km	10.0 km	15.0 km
Neighbors	NS	NS	NS	+(3)***	+(2)***	+(2)***

Table 1: Counts of arriving foundresses in *Ficus petiolaris* syconia as a function of the number of neighboring conspecific figs within different distances (*r*). Table elements indicate the effect (+ or -), % variance explained (in parentheses), and significance at the 0.05 (*), 0.01 (**), and 0.001 (***) levels. Elements with “NS” were not significant.

Scale at which neighbors defined (r)							
Ind. Variable	0.1 km	0.5 km	1.0 km	5.0 km	10.0 km	15.0 km	
Neighbors	NS	NS	NS	NS	NS	NS	
Foundresses	+(6)***	+(6)***	+(7)***	+(8)***	+(8)***	+(8)***	
Neighbors \times Foundresses	NS	NS	NS	-(1)*	NS	NS	

Table 2: Estimates of pollinator production in *Ficus petiolaris* syconia as a function of the number of neighboring conspecific figs within different distances (r) and the number of arriving foundress pollinators. Table elements indicate the effect (+ or -), % variance explained (in parentheses), and significance at the 0.05 (*), 0.01 (**), and 0.001 (***) levels. Elements with “NS” were not significant.

Scale at which neighbors defined (r)		0.1 km	0.5 km	1.0 km	5.0 km	10.0 km	15.0 km
Ind. Variable							
Neighbors		NS	NS	NS	-(7)***	-(9)***	-(8)***
Foundresses		+(7)***	NS	NS	NS	-(3)**	-(3)*
Neighbors \times Foundresses		-(3)*	NS	NS	NS	+(5)***	+(6)***

Table 3: Estimates of seed production in *Ficus petiolaris* syconia as a function of the number of neighboring conspecific figs within different distances (r) and the number of arriving foundress pollinators. Table elements indicate the effect (+ or -), % variance explained (in parentheses), and significance at the 0.05 (*), 0.01 (**), and 0.001 (***) levels. Elements with “NS” were not significant.

Scale at which neighbors defined (r)							
Ind. Variable	0.1 km	0.5 km	1.0 km	5.0 km	10.0 km	15.0 km	
Neighbors	-(3)***	-(10)***	-(9)***	-(2)***	-(1)**	-(1)**	
Foundresses	-(6)***	-(5)***	-(5)***	-(3)***	-(2)***	-(2)**	
Neighbors \times Foundresses	+(3)***	+(2)***	+(2)***	+(1)**	NS	NS	

Table 4: Estimates of exploiter production in *Ficus petiolaris* syconia as a function of the number of neighboring conspecific figs within different distances (r) and the number of arriving foundress pollinators. Table elements indicate the effect (+ or -), % variance explained (in parentheses), and significance at the 0.05 (*), 0.01 (**), and 0.001 (***) levels. Elements with “NS” were not significant.

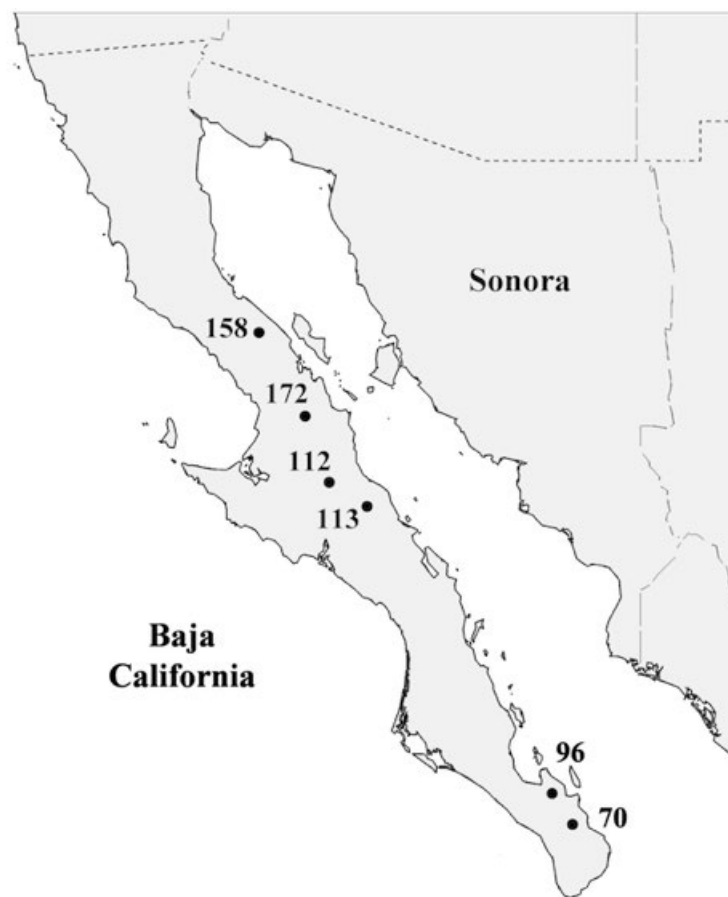


Figure 1: Six *Ficus petiolaris* populations in which trees were mapped and syconia were collected along peninsular Baja California, Mexico.

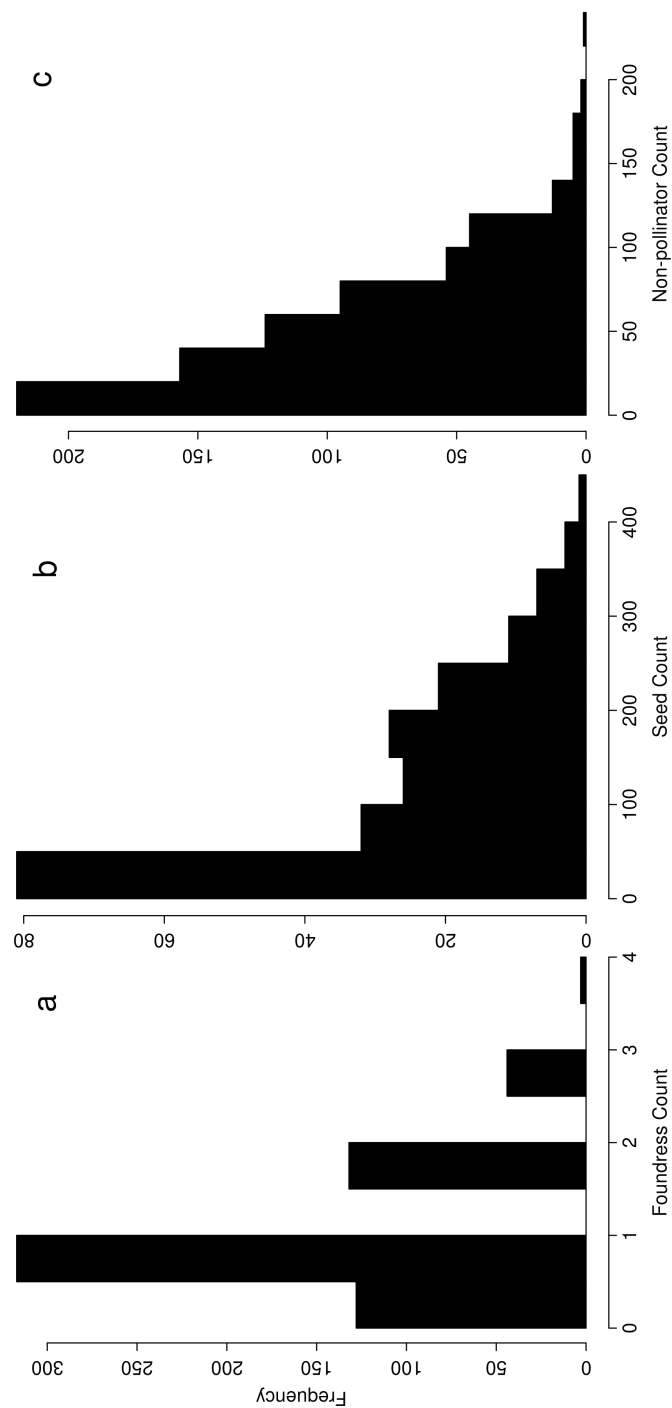


Figure 2: Histogram showing counts of pollinating foundress wasps (a), seeds (b), and exploiter fig wasps (c) collected from mature, male-phase syconia of *Ficus petiolaris* trees

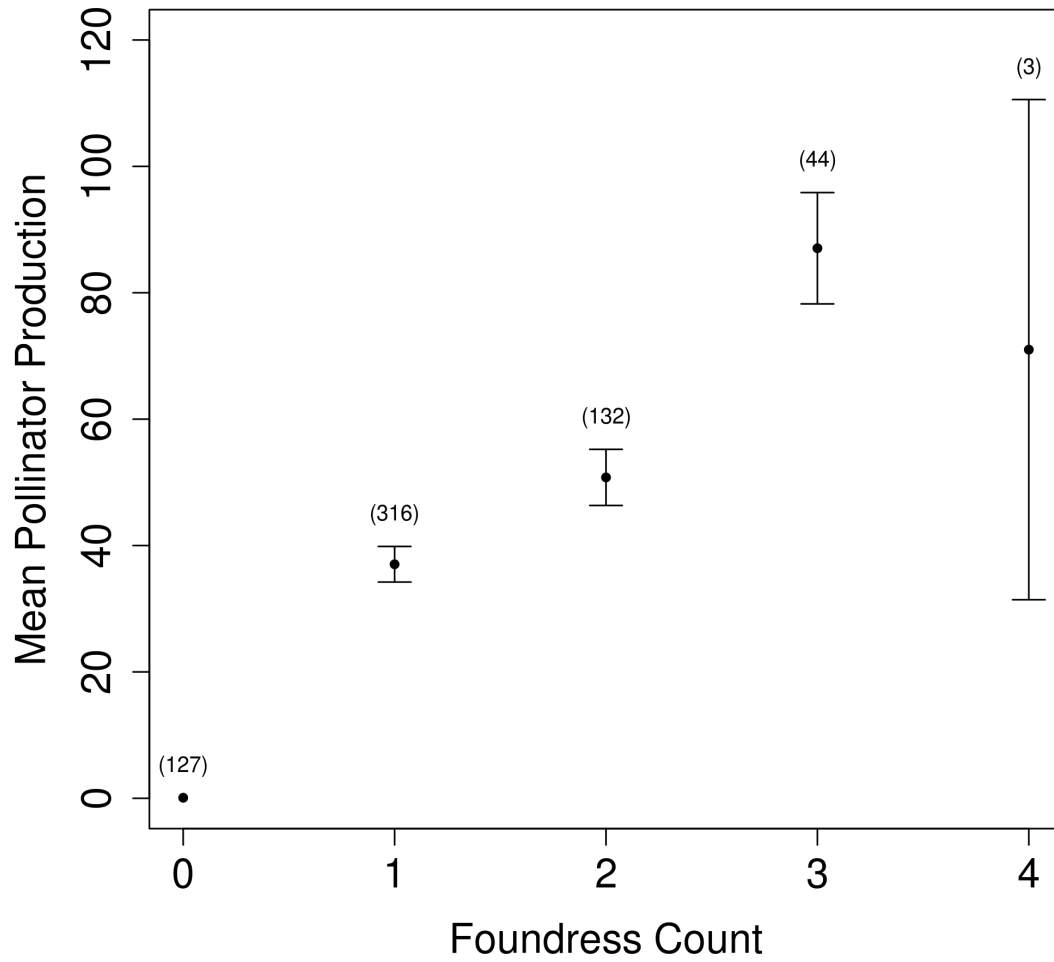


Figure 3: Mean pollinator production within fig syconia of *Ficus petiolaris* as a function of the number of arriving pollinating foundresses. Error bars show standard errors around the means. Numbers in parentheses show the number of syconia from which each number of foundresses was obtained.

CHAPTER IV. TRADE-OFFS AND COEXISTENCE: A LOTTERY MODEL APPLIED TO FIG WASP COMMUNITIES

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Abstract

Ecological communities in which organisms complete their life cycles on discrete, ephemeral, patches are common and often support a large number of species. Such communities include the myriad species of fig wasps competing for access to oviposition sites on 750+ species of figs. Oviposition occurs within fig syconia (enclosed inflorescences), which develop sporadically, and usually in synchrony on a fig crown. Between bouts of reproduction, figs have periods of inactivity in which syconia are absent, so eclosing wasps must disperse to new and receptive figs. Fig species typically host a single species of pollinating fig wasp, but multiple species of host-specific non-pollinators. Because non-pollinator species are often closely related, have similar life histories, and compete for identical resources, understanding their coexistence is challenging given that competitive exclusion is expected. We simulate a lottery model employing a temporal storage effect wherein species competitive ability is determined by a trade-off between its fecundity and its ability to disperse. We show the temporal storage effect leads to long-term coexistence

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under a wide range of biologically realistic parameter values. For a subset of parameter values, we use individual-based modeling to show that when species character traits evolve, trait divergence can result among competitors. We discuss the implications of this coexistence mechanism for empirical studies of fig wasp communities and ephemeral patch systems.

Introduction

Ecological communities in which organisms complete their life cycles on discrete, ephemeral patches often support a large number of species (e.g., Atkinson and Shorrocks, 1981; Hartley and Shorrocks, 2002). These discrete and ephemeral patches include carrion, fungi, dung, or fruits, and many theoretical and empirical studies have focused on understanding the mechanisms by which species using these resources are able to coexist (e.g., Shorrocks et al., 1979; Atkinson and Shorrocks, 1981; Chesson, 2000; Woodcock et al., 2002). Most studies of coexistence in ephemeral patches focus on the mechanism of aggregation (Chesson, 2000). Animals that aggregate in ephemeral patches are often modeled using Lotka-Volterra equations (e.g., Shorrocks et al., 1979) or the competition equations of Hassell and Comins (e.g., Hassell and Comins, 1976; Atkinson and Shorrocks, 1981). In these models, the growth rate of each species is depressed by competition coefficients such that increasing the density of individuals within a patch will decrease population growth for one or more species. Conspecific aggregation intensifies intraspecific competition relative to interspecific competition, potentially leading to competitive coexistence (e.g., Atkinson and Shorrocks, 1981; Ives, 1988; Sevenster, 1996; Hartley and Shorrocks, 2002). While this is an effective way to model resource competition within many ephemeral patch types, the conceptual framework is less effective for patches in which all individuals preempt a fixed number of discrete resources. For example, some insects require a single discrete resource, such as a host plant's seed, to complete their development. When every individual uses a single discrete resource, preemption of that

resource likely has an equivalent effect on all other individuals in the patch, regardless of their species. Species-specific plant-insect interactions of this type include camellia and associated weevils (Saito and Suzuki, 1982), a globeflower and its associated fly (Després and Jaeger, 1999), a palm and its associated weevil (Alves-Costa and Knogge, 2005), and many species of figs (genus *Ficus*) and the wasps that they host. In these interactions, the discrete nature of resources within patches makes within patch aggregation less likely to result in coexistence among competing species, although aggregation may facilitate coexistence at the among patch level (e.g., Ives, 1991). For this reason, we consider an additional mechanism that may significantly facilitate coexistence in ephemeral patch systems, especially those in which resources within patches are discrete. Using a community of non-pollinator fig wasps as a model system, we introduce an alternative explanation for coexistence among competitors that relies on a trade-off between fecundity and dispersal ability, and variation in travel distance among patches.

The obligate mutualism involving figs (750+ species) and fig wasps is a textbook example of a highly-coevolved mutually beneficial interaction in which figs require species-specific fig wasps for pollination, and wasps require patchy, ephemeral, fig ovules for larval development. Large numbers of these ovules are contained within a fig syconia (enclosed inflorescences; hereafter “fruits”) with a single fig wasp larva galling an individual ovule. In addition to pollinating fig wasps, figs often support a diversity of host-species-specific non-pollinating wasps, many of which use fig ovules in seemingly the same way. The discrete nature of fig ovule resources makes aggregation an unlikely mechanism for explaining how multiple species of fig wasps can coexist on a single host fig species. Instead of the interference competition invoked in aggregative competition models, interactions among fig wasps competing for ovules is better understood as exploitative competition wherein ovipositing female wasps compete by maximizing their rates of oviposition. The exploitative nature and discrete resource use involved in fig wasp interactions makes a

lottery competition model more applicable than an aggregation model for standing fig wasp diversity. In a lottery model, individuals compete for a limited number of discrete resources (usually empty habitat, but here single ovules), and once a resource is claimed, an individual cannot be usurped from it (Sale, 1978). The probability that a particular species will claim a discrete resource is determined by the number and fecundity of individuals within that species relative to other species in the community (Warner and Chesson, 1985). Coexistence in lottery systems can be maintained when generations are overlapping and growth rates fluctuate such that each species is competitively superior some of the time (Chesson and Warner, 1981; Chesson, 1982).

It is the coexistence of multiple species of ecologically similar non-pollinators exploiting a single resource that we wish to explain. We ask whether variability in competitive dominance induced by temporal variation in the spatial distribution of resources can lead to coexistence when there is a trade-off between fecundity and dispersal ability. This work is framed with respect to the diverse non-pollinating fig wasp community associated with a single fig host species as representative of ephemeral patch systems in which resources are discrete. To investigate this proposed coexistence mechanism, we use a population-level model. We show that variability in competitive dominance among fig wasp species is induced by variation in the minimum dispersal distance between a wasp's natal fig and figs receptive for wasp oviposition. This variation can lead to coexistence when there is a trade-off between wasp fecundity and dispersal ability, and subsets of wasp populations are stored in fruits over multiple wasp cohorts. Using an individual-based adaptive dynamics model, we additionally examine the consequences of individual demographic variation and the evolution of fecundity and dispersal traits. We show that evolution can lead to trait divergence in the trade-off between wasp fecundity and dispersal ability.

Non-pollinating fig wasp coexistence

Fig wasps (superfamily Chalcidoidea) include both a monophyletic group of obligate pollinators (family Agaonidae) and a diverse group of non-pollinating exploiters (multiple families), most of which are host-specific (Weiblen, 2002). At receptivity, the female flowers within fig syconia release volatile cues that attract both pollinating and non-pollinating wasps. Previously-inseminated pollinators enter the fruit through a small opening (ostiole) and lay their eggs into a subset of ovules. Non-pollinators also lay eggs into fig ovules, in some cases by entering through the ostiole like the pollinators, or more generally by ovipositing through fruit walls (e.g., Kerdelhué et al., 2000; Proffitt et al., 2007; Ranganathan et al., 2010). In monoecious figs, which we model here, wasp offspring mature over several weeks before emerging from ovules and mating within their natal fruit. Upon emergence from the natal fruit, females must disperse to new receptive fruit to lay their eggs.

In addition to the well-known mutualism involving pollinating wasps, the community of fig wasps associated with a single fig host can contain up to 30 species of host-specific non-pollinators, often developing within the same fruits (Compton and Hawkins, 1992). How can this diversity of coexisting non-pollinating wasps be maintained where competitive exclusion over access to ovules might be expected? While some fig wasps are parasitoids, the majority gall ovules, and several hypotheses have been proposed to explain galler coexistence, including differences in the mode (e.g., Kerdelhué et al., 2000; Ghara et al., 2011) and timing (e.g., Kerdelhué et al., 2000; Ghara and Borges, 2010) of oviposition. While these difference likely promote niche partitioning to some degree, it is unclear how these differences among species could prevent competitive exclusion when ovule resources limit fig wasp population growth. The identification of a more general mechanism explaining the coexistence and diversity of non-pollinating fig wasps remains a challenge. Rather than focusing on how non-pollinating wasps differ in their exact use

of the fig fruit, we suggest a coexistence mechanism dependent upon the phenology of host figs and a fundamental trade-off between wasp dispersal ability and fecundity.

Variation in fig resource availability

Except where populations are sparse or fragmented (e.g., Ramírez, 1970; Bronstein, 1989; Gates and Nason, 2012), fruit development within the crown of a fig usually occurs in synchrony, presumably to increase the total amount of volatile cues available to pollinators (Bronstein, 1989) and promote outcrossing (Bronstein and Patel, 1992; McPherson, 2005). Because the developmental stages at which fruits are receptive to wasps and when wasps eclose (emerge) are completely separated in time, fig wasps must leave their natal fig to locate a fig bearing receptive fruit. Between bouts of reproductive activity, figs can go through periods of reproductive inactivity in which no fruiting occurs for months or even years (Bronstein, 1989; Windsor et al., 1989). The initiation of fig fruit development has been described as sporadic and aseasonal (Kjellberg and Maurice, 1989), though in some cases it may be seasonally variable (Bronstein and Patel, 1992). For wasps that must migrate from their natal fig to another receptive fig, this unpredictable phenology introduces much stochasticity in the distance wasps must disperse to successfully locate receptive figs. As such, Compton et al. (1994) and McPherson (2005) have argued that within-crown fruiting synchrony should limit wasp fitness due to dispersal mortality. During periods in which receptive fruits are far away in time or space, short-lived and poorly dispersing wasps will be less likely to find receptive fruits for oviposition; hence their reproduction will be lowered. In contrast, when receptive fruits are very close, dispersal ability will be less important, and the most fecund wasps will be expected to benefit even if their dispersal abilities are poor. We suggest that the landscape-level variability inherent in the availability of fig ovules can promote coexistence among multiple types of wasps that specialize to different degrees on fecundity or dispersal ability. This coexistence occurs because the competitive superiority of non-

pollinating wasp species changes as the distance to the nearest receptive fig changes over time, and periods wherein wasp species experience unfavorable conditions for accessing receptive figs are buffered by population storage in figs of wasps yet to emerge.

Coexistence by the storage effect

The storage effect is a mechanism by which ecologically similar species are able to coexist within a community. This mechanism relies on overlapping generations and each species having a unique response to environmental variability such that every species is competitively superior some of the time. Gains from favorable environments are stored in the population to buffer against the effects of unfavorable environmental conditions, and, given a sufficient amount of environmental variation, all populations have a positive growth rate when rare and intraspecific competition is low (Chesson and Warner, 1981; Chesson, 1982). Thus, in addition to varying competitive dominance, the storage of individuals is critical to coexistence by preventing extinction when environmental conditions are unfavorable. As such, empirical studies have found evidence supporting the storage effect as a coexistence mechanism in species that maintain very long-term population storage. These species include long-lived woody plants (e.g., Kelly and Bowler, 2002), desert annuals with persistent seed banks (e.g., Pake and Venable, 1995; Angert et al., 2009), and freshwater zooplankton with dormant stages (e.g., Cáceres, 1997, 1998). Non-pollinating fig wasps do not maintain such long-term population storage; both their larval and adult stages are completed on a timescale of weeks instead of years. But in contrast to the relatively slow rate of change in resource availability experienced by woody plants and freshwater zooplankton, new resources for fig wasps (ovules) rapidly become available with every newly receptive fig, and the emergence of a single cohort of non-pollinators may extend over multiple inceptions of fig receptivity on the landscape of a fig population. Here we show that this overlap in generations is sufficient to maintain stable coexistence in a manner similar to that of species with longer life histories that

compete over more spatially and temporally persistent resources.

The population model

We use three equations to model multiple, co-occurring species of non-pollinating fig wasps. The first equation describes the probability distribution of the minimum distance that a fig wasp needs to travel to successfully disperse to a receptive fig. The variance in this distribution provides the environmental variation for promoting coexistence. The second equation describes the probability that a wasp will successfully disperse from its natal fig to a new fig that is receptive for wasp oviposition. This probability is a function of the minimum travel distance described by the first equation and of a wasp's species-specific dispersal ability. The third equation models how the population size of wasp species i changes from time t to time $t + 1$. These equations are used in numerical simulations to explore the parameter values facilitating species coexistence and to determine if this coexistence is associated with differences among species in fecundity-dispersal trade-offs. They also form the basis for the individual-based model described below. These models track newly eclosed adult wasps that are living within fig fruits prior to dispersal, because this is the stage that is commonly censused in the field.

Distribution of minimum travel distance

A Poisson process describes independent events occurring over a continuous distance of space or time. The probability distribution of the first event of a Poisson process occurring over a particular length of space or time is described by an exponential distribution. As such, we use an exponential distribution to model the probability density of the distance from a wasp's natal fig to the nearest receptive fig (r_{dis}), which contains ovules into which wasps will oviposit in a lottery competition,

$$P(r_{dis}(t) = x) = \frac{1}{\alpha} e^{-\frac{1}{\alpha}x}. \quad (1)$$

The parameter α is the expected distance to the nearest receptive fig. Here it is estimated by fitting an exponential function to data on the minimum distance between figs with emerging fig-wasps and figs with receptive fruit at particular moments in time (Figure 1).

Probability of wasp dispersal success

Diffusion equations have long been used to model patterns of insect dispersal (see Okubo and Kareiva, 2001, for review). The process of diffusion arises as individuals move in a random walk (or flight) around their environment. We model the fig wasp environment as a two-dimensional landscape on which non-pollinating fig wasps take random flights from their natal fig. For a receptive fig located $r_{dis}(t)$ from a wasp's natal fig, the probability of successful dispersal for a wasp of species i at time t is

$$c_i(t) = \frac{r_{tar}}{\pi l_i} \Gamma \left(0, \frac{r_{dis}^2(t)}{2l_i\psi_i} \right) \quad (2)$$

(based on an approximation derived by Friedrich, 2008). In the above, r_{tar} refers to the radius of the wasp's target, a receptive fig. Here we model the target as the radius of the cloud of volatile cues surrounding the fig, which we assume to be a circle, as recent empirical research has shown that non-pollinating wasps use chemical mediation to locate receptive host figs (Proffitt et al., 2007). We do not know of any empirical estimates of r_{tar} , but we found coexistence ranges to be extremely robust to different values. The parameter ψ_i describes the total length of the path that a wasp of species i takes on its flight, and depends both on the velocity and duration of the random flight. Differences in ψ_i among species model different dispersal abilities. We assume that species differences in this path length are related to differences in their longevity and dispersal speed. The variable l_i describes the walk persistence length of species i ; that is, the tendency for a wasp moving in a given direction to continue in that direction (see Friedrich, 2008,

for details). For very small values of r_{dis} (when the natal fig and receptive fig are very close), equation (2) can lead to values in which $c_i > 1$. When this occurred, c_i values were truncated to unity.

Change in wasp population size over time

We describe change in the population sizes of non-pollinating wasp species using a lottery model in which φ new ovules are available for oviposition at each time step. We define $P_i(t)$ as the total population density of adult wasps of species i living inside fig fruits at time t . Following Chesson and Warner (1981) and Chesson (1982), we define β_i to be the maximum possible number of offspring (hereafter “fecundity”) produced by an individual wasp of species i . To describe the number of offspring that we expect a female of species i to produce in the absence of competition, we multiply its fecundity by the probability of it successfully dispersing to a receptive fig ($c_i(t)$; eqn (2)), giving a realized reproduction of $\beta_i^*(t) = \beta_i c_i(t)$ at time t . We use two additional parameters to model the development of larvae within fig fruit. One of these parameters, τ , is the wasp development time from oviposition to adulthood, which is assumed to be constant across wasp species developing within syconia of the same host fig species. The other is δ_i , the probability that adult wasps of species i emerge from the ovules in which they developed at any time step. For k different wasp species, we arrive at the third equation of our model, the population size of wasp species i at time $t + 1$ is,

$$P_i(t + 1) = (1 - \delta_i)P_i(t) + \varphi \left(\frac{\delta_i \beta_i^*(t - \tau) P_i(t - \tau)}{\sum_{i=1}^k \delta_i \beta_i^*(t - \tau) P_i(t - \tau)} \right). \quad (3)$$

For simplicity, we focus on the case in which $k = 2$ non-pollinating wasp species, but exploratory simulations show that this model can predict coexistence of > 2 species.

As in Chesson (1982), the expression in parentheses in the second term of equation (3) models a lottery competition. Mature wasps compete for oviposition space in φ ovules;

the number of adults completing development during time step t is determined by the realized reproduction (β_i^*) and density of the population (P_i) of adult wasps τ time steps earlier. The storage effect (Warner and Chesson, 1985) is made possible by the first term of equation (3), wherein a single cohort of wasps may persist as developing larvae in their ovules over multiple time steps. This term is critical to facilitating coexistence because it limits sharp population decline during unfavorable conditions by allowing the overlapping of generations. In our model, δ_i is the proportion of adult wasps that exit from their ovules at every time step, while a proportion $(1 - \delta_i)$ of adult wasps remain waiting to exit.

To show that non-pollinating wasp species may coexist, we need to show that the mean geometric growth rate for each species i is positive when $P_i(t)$ is low (Turelli, 1978). As pointed out by Chesson and Warner (1981), this is not entirely sufficient because it may allow coexistence when $P_i(t)$ is unrealistically low for a standing population. To avoid unrealistically low population sizes, we define species as coexisting when the mean rate of growth for each species is positive

$$E \left[\ln \left(\frac{P_i(t+1)}{P_i(t)} \right) \right] > 0, \quad (4)$$

and when the minimum proportions of each species persists above some threshold, $1/m$, for all time steps,

$$\frac{P_i(t)}{\sum_{i=1}^k P_i(t)} > \frac{1}{m}. \quad (5)$$

Population model simulations

The coexistence of species described by the population model was examined via computer simulation with values of model parameters determined by available information on fig wasp fecundity and dispersal. In a recent study of comparative life-history traits from a community of eight non-pollinating fig wasp species, Ghara and Borges (2010) found

the egg loads (β_i) of individuals to range between ca 59 and 263. In our model, β_i values were randomly selected from a uniform distribution between 50 and 300 for each species. To our knowledge, no ecological data exist that describe the velocity, walk length, or walk persistence of dispersing non-pollinating fig wasps, but empirical studies of pollinating fig wasps estimate that pollinators can regularly disperse 5800-14200 meters (Nason et al., 1998) or farther (Ahmed et al., 2009). This dispersal in pollinators is largely wind-borne, but it is not known to what extent this is also the case for non-pollinators. In our model, we randomly selected ψ_i values between 1000-20000 for each species.

For a single set of β_i and ψ_i values, coexistence was defined as satisfying the conditions of inequalities (4) and (5) ($m = 1000$) over 52000 time steps (1000 years, wherein we model time steps as a one week period) after allowing the simulation to equilibrate for 100 time steps. To ensure that 52000 time steps was sufficient to judge coexistence, we removed the coexistence-promoting environmental variability by setting $r_{dis}(t) = \alpha$ for all time steps and verified that the conditions of inequalities (4) and (5) were never satisfied for ecologically-distinct species (i.e., species with different β_i, ψ_i). We likewise removed the population storage required for long-term coexistence by setting δ_i equal to unity for all species and verified that coexistence criteria were never satisfied.

Default values for other parameters can be found in Table 1; we believe these to be biologically realistic. In the case of α in equation (1), we used geographic coordinates and phenological data from a Mexican population of *Ficus petiolaris* figs to arrive at a reasonable parameter value using maximum likelihood estimation (Figure 1; $\alpha = 714.2857$). To ensure that our results were not highly sensitive to these specific model parameters, we simulated 52000 time steps at randomly selected values of β_i and ψ_i over a variety of different values of α (100, 200, \dots , 1900, 2000), τ (3, 4, \dots , 9, 10), δ_i (0.70, 0.72, \dots , 0.98, 1.00), l_i (10, 100, 1000, 10000), and r_{tar} (10, 100, 1000, 10000).

To simulate two species of non-pollinating fig wasps (C code available upon request),

we began by randomly selecting values for β_i and ψ_i , then setting the abundance of each species to 5000 for τ time steps so that $P_1(0) = P_2(0)$. Every subsequent time step of the simulation proceeded by 1) randomly selecting a value for $r_{dis}(t)$ from the probability distribution described in equation (1), then 2) calculating $\beta_i^*(t)$ for each species of wasp. These values were then 3) used in equation (3) to determine $P_i(t+1)$. When all time steps had finished, 4) the mean geometric growth rate was calculated, as was 5) the minimum proportional abundance of both species over the course of the simulation. If and only if the conditions in inequalities (4) and (5) were satisfied, we concluded that coexistence was possible at the parameter values used. We simulated 10000 randomly selected β_i and ψ_i values for all previously mentioned values of α , τ , δ_i , l_i , and r_{tar} values.

Individual-based model simulations

To explore the consequences of demographic stochasticity, evolution, and individual within-species variation in fecundity and dispersal ability, we constructed an individual-based model (IBM) of the mechanism described above. In the IBM, we replicated the population-level simulation as closely as possible while allowing for individual within-species variation. At each time step, non-pollinating fig wasps in the IBM disperse to new ovules, which are located at a distance of $r_{dis}(t)$ from their natal ovules (equation (1)). As in the population model, equation (2) determines the probability that an individual wasp successfully disperses, but the IBM allows for individual variation about the species-specific expected fecundity (β_i) and dispersal ability (ψ_i). In the IBM, each successfully dispersing wasp can produce some number of offspring as determined by the individual wasp's fecundity, β_{wasp} . These offspring compete in a lottery along with the offspring of other successfully dispersing wasps wherein each offspring has an equal chance of occupying one of φ ovules. After the lottery competition, offspring develop over τ time steps, after which each individual wasp exits its natal ovule with a probability of $(1 - \delta_i)$ at every subsequent t .

Empirical research has shown rapid adaptive evolution to be influential to ecological dynamics, and many models of interspecific interactions have begun to incorporate adaptive evolution (Thompson, 1998; Pelletier et al., 2009). Here we allow hereditary variation to influence the evolution of species-specific expected fecundity and dispersal ability. Following Wood and Ackland (2007), we prevent unrealistic evolution by constraining individuals not to exceed a set maximum expected product of fecundity and dispersal probability ($E[\beta^*]$). We considered 5 different maximum $E[\beta^*]$ values, and for each, we found the trade-off line defined by $\beta_{wasp}, \psi_{wasp}$ combinations that yield the maximum $E[\beta^*]$ at the expected inter-tree distance ($E[r_{dis}] = \alpha = 714.2857$) (Figure 2). In the simulations, trait values for the offspring of individuals were selected from a random normal distribution of parents such that $\beta_{offspring} = N(\beta_{parent}, 1)$ and $\psi_{offspring} = N(\psi_{parent}, 10)$; fecundity values were rounded to the nearest integer. If after selection the trait values were above the trade-off line, then either fecundity or dispersal ability was randomly selected with equal likelihood to be lowered so that $E[\beta^*]$ fell back on the trade-off line.

To begin a single simulation run (Figure 3), initial fecundity and dispersal ability values are selected for each species from anywhere within the ranges of $\beta = 50 - 300$ and $\psi = 1000 - 20000$. Combinations of fecundity and dispersal ability values that result in $E[\beta^*]$ values greater than allowed are immediately rejected, and new values are selected before the simulation run proceeds. When acceptable values are found for each species, 10000 individuals are randomly assigned to a species with equal likelihood, and all individuals within a species are assigned the same fecundity and dispersal ability. The developmental stage of each individual is randomly assigned to a week of development time from 0 to τ . For each maximum $E[\beta^*]$ trade-off line (Figure 2), we run 1000 simulations, each with 5200 time steps, wherein both species are allowed to evolve, and 1000 simulations wherein no evolution occurs. In the latter case, trait values of offspring are

identical to those of parents and trait values are uniform within species. We compare the probability of long-term coexistence in communities that are allowed to evolve and communities in which no evolution occurs. If simulations in which evolution is permitted result in a higher proportion of communities with long-term coexistence, our model suggests that evolution may facilitate coexistence in the presence of the storage effect. For simulations in which evolution is allowed, we also calculate the mean change in trait difference between species per time step. If species are diverging ecologically in one or both traits, this divergence will be reflected in a mean increase in trait difference. If species are not diverging ecologically, no trend is to be expected in the difference between species trait values, or trait values may converge. If simulations in which species evolve result in a higher rate of trait divergence, our model suggests that the storage effect may facilitate evolutionary divergence.

Results

Population model simulations

Over all simulations, the pattern of coexistence across $\beta_i - \psi_i$ space was qualitatively the same. Two species were able to coexist only if there was an inverse relationship between β_i and ψ_i , and simulations in which one species was superior to the other in both of these randomly selected values lead to the extinction of the inferior competitor. Although coexistence criteria were met at least some of the time for all parameter combinations (with the exception of $\delta_i = 1$, which removed all population storage), some parameter values were more likely to facilitate coexistence. Coexistence became less likely as the expected dispersal distance to the nearest tree (α) increased (Figure 4A), and more likely as development time (τ) increased (Figure 4B). The probability of coexistence decreased as the proportion of wasps stored in each time step was reduced (Figure 4C). The relationship between coexistence and flight persistence did not have a clear directional trend (Figure 4D), and coexistence was only slightly augmented with an increase in the size of

the attractive cloud of volatiles around the fig (Figure 4E).

To visualize the range of β_i and ψ_i values that one species could take given the values of a second, we set $\beta_1 = 150$ and $\psi_1 = 10000$ at default parameters values, then tested whether or not species could coexist when $\beta_2 = (50, 51, \dots, 299, 300)$ and $\psi_2 = (1, 2, \dots, 9990, 20000)$. A plot showing the interaction between β_i and ψ_i coexistence values reveals a pattern that has a concave parabolic shape that widens at the ends and shrinks to a point in the center where $\beta_1 = \beta_2$ and $\psi_1 = \psi_2$ (Figure 5). This pattern of coexistence was retained over multiple simulated parameter combinations (results not shown).

Individual-based model simulations

The probability of coexistence for wasp species with randomly selected life-history traits of fecundity and dispersal ability increased with $E[\beta^*]$ both when traits were fixed and allowed to evolve (Figure 6). The probability of coexistence increased more rapidly with $E[\beta^*]$ in simulations wherein no evolution occurred, but this increase also leveled off more quickly than in simulations with evolving populations. In the latter, the probability of coexistence increased dramatically when $E[\beta^*] > 25$ (Figure 6).

For all values of $E[\beta^*]$, the mean difference in species fecundity and dispersal ability increased over time from one time step to the next (Figure 7). For species fecundity values, this increase was uniform for all levels of $E[\beta^*]$, with an overall mean increase of ca 0.0069 per time step. In contrast, the divergence in dispersal ability between species was more rapid for intermediate values of $E[\beta^*]$, with its most rapid increase at ca 0.4106 when $E[\beta^*] = 35$, and its least rapid increase of ca 0.0881 when $E[\beta^*] = 5$. While the difference in fecundity and dispersal ability values generally increased over time in simulated species, both species tended to evolve toward higher fecundity values at the cost of absolute dispersal ability. This trend was true across all trade-off lines simulated.

Discussion

Here we model an ephemeral patch system in which the minimum travel distance for successful dispersal to a new patch varies over time. With this varying travel distance, the probability of successful dispersal also varies, and species that use ephemeral patches as a resource for larval development face a trade-off in the degree to which they invest in dispersal ability and fecundity. When combined with Chesson's storage effect model of coexistence (Chesson and Warner, 1981; Chesson, 1982), this trade-off can result in multiple coexisting species that specialize to different degrees on dispersal ability and fecundity. To model this mechanism, we use a lottery competition focusing on the interactions within a community of non-pollinating fig wasps that compete for access to the ovules of figs for larval development. We show that variation in the minimum travel distances facilitates coexistence among competing wasp species with different life history trade-offs for dispersal ability and fecundity. These results offer an explanation for the extensive and widespread diversity of non-pollinating fig wasps that use fig fruits as a resource for larval development. Finally, we show that this coexistence mechanism can lead to trait divergence under the assumptions of our IBM.

Because of their remarkable diversity, non-pollinating fig-wasp communities have been the focus of multiple ecological studies. An interesting feature of this diversity is the variability of non-pollinator species richness across taxonomic and geographical scales. Among South African fig species, for example, non-pollinator species richness has been found to range between 3 and 30 (Compton and Hawkins, 1992), and an extreme amount of variability in wasp species richness has been observed among individuals within species of figs as well (Hawkins and Compton, 1992). In a study of non-pollinating wasp diversity among fig species, Compton and Hawkins (1992) suggest that variability in species richness may be due to historical factors that limit the richness of non-pollinators that develop in a particular fig species. A similar study showed evidence for the under-

saturation of fig-wasp communities, and the variability of local non-pollinator species richness led the authors to suggest that wasp life histories strongly constrain host-finding ability (Hawkins and Compton, 1992). Our model shows how this constraint can be a coexistence-promoting mechanism when fig phenology is also considered. Because individual figs remain unreceptive to fig wasps for an extended length of time and become receptive for only a short period of time, the distance over which a fig wasp is required to travel to reach a receptive tree can vary greatly from one natal fig and wasp generation to the next. Our results show that a trade-off between dispersal ability and fecundity can provide a mechanism for coexistence in such a variable landscape. We hypothesize that when the travel distance to a receptive tree is low, wasps that invest more resources in fecundity will have the highest fitness, and when travel distance is far, wasps that are especially good dispersers will be favored.

Dispersal-fecundity trade-offs in insects

Many insects face a trade-off between fecundity and longevity at both intraspecific (e.g., Rose, 1984; Kaitala, 1991; Tatar et al., 1993; Ellers and Alphen, 1997) and interspecific (e.g., Jervis et al., 2001; Pexton and Mayhew, 2002; Jervis et al., 2007) levels. The ovigeny index (OI; Jervis et al., 2001) can be used as an empirical estimate of this trade-off expressed as the ratio of fully mature eggs at adult emergence over lifetime potential fecundity. A high OI describes an insect with all eggs mature upon adult emergence, while a low OI describes an insect with few eggs ready to lay. A negative correlation between OI and longevity is both empirically supported (e.g., Jervis et al., 2007) and intuitive. If the number of mature eggs upon adult emergence is small relative to lifetime potential fecundity, time is needed for new eggs to be produced, so greater longevity should be expected. Compton et al. (1994) note that the probability of successful fig colonization will be affected by the longevity of dispersing female wasps. If some fig wasps are more long-lived than their competitors, we can expect them to have more time to search

for suitable oviposition sites. Because the mechanism of coexistence we propose herein relies on a trade-off between fecundity and dispersal ability, we might predict a negative correlation between the relative egg loads and OI values of competing non-pollinators in fig-wasp communities. Unfortunately, non-pollinating gallers in fig wasp communities for which OI values have been measured appear to be mostly pro-ovigenic (e.g., Compton et al., 1994; Ghara and Borges, 2010), so OI values for these communities may lack the variation required for their use as a metric of relative dispersal ability. In contrast, non-pollinating wasps that are parasitoids of pollinators and gallers have been found to be mostly syn-ovigenic and more long-lived (e.g., Compton et al., 1994; Ghara and Borges, 2010), which is likely adaptive for finding hosts (Compton et al., 1994).

A large number of mature eggs at emergence has been suggested to limit insect mobility in other ways (see Jervis et al., 2005, for review), such as by increasing abdominal mass (e.g., Sattler, 1991) or reducing body space for thoracic muscles (e.g., Kaitala, 1988). Both of these characteristics of morphology would be interesting avenues of research in fig wasps. Unfortunately, because fig wasps are extremely small and often far-dispersing (Nason et al., 1998; Ahmed et al., 2009; Yu et al., 2010), direct measures of individual mobility can be difficult to obtain. Recently, Ghara and Borges (2010) examined life history traits of fig wasps in the community ovipositing in *F. racemosa*, which included three species of galling non-pollinators. They found variation in fecundity and longevity among these species, and while they did not measure the dispersal ability of species in the community, they noted that the abundances of species varied both locally and seasonally. Ghara and Borges (2010) suggest that the life-history traits of community members will be affected by spatio-temporal variation in figs.

Within a community of fig wasps associated with the same species of fig, we can predict spatio-temporal patterns of species distribution among trees. The variance in abundance of high fecundity, high OI, wasps among figs in a population is likely to be

highest at the large spatial scales, resulting in clumped spatial distributions. The reason for this high variance is that these wasps will be more severely limited by their dispersal abilities. Remote fig trees are more likely to escape exploitation from these wasps, but fig trees in aggregation will likely experience especially high exploitation even if wasp dispersal ability is low. In contrast, fig wasps that are adept dispersers are likely to be more evenly distributed across the landscape. The proportion of low fecundity, low OI, wasps will not drop as severely with fig remoteness because dispersal limitation will be less severe with distance.

Empirical studies of ant-plant symbioses suggest that a trade-off between dispersal ability and fecundity can lead to coexistence given spatially variable host plant density in competing insect species. *Cordia nodosa* is a tropical plant that is inhabited by ant colonies of the genera *Allomerus* and *Azteca* (Yu et al., 2001, 2004). The two ant genera coexist among, but not within, individual plants. At low host-plant densities, the farther dispersing *Azteca* species are represented by colonies that occur in higher relative abundances and are evenly distributed over multiple spatial scales (Yu et al., 2004). In contrast, Yu et al. (2004) found that colonies of a single species of *Allomerus* are twice as fecund as their *Azteca* competitors, but foundresses of this species have a poorer dispersal ability, and their distribution was significantly clumped at spatial scales ≤ 100 meters.

Individual-based model and evolutionary dynamics

A comprehensive understanding of non-pollinator fig-wasp diversity will almost certainly require an understanding of many ecological and evolutionary processes. Although the storage effect is an important mechanism for maintaining biodiversity in a variety of taxa (e.g., Angert et al., 2009; Kelly and Bowler, 2002; Cáceres, 1997), how evolution acts to promote or hinder the coexistence of competitors maintained by the storage effect has been largely unexplored (but see Snyder and Adler, 2011; Svardal et al., 2011; Abrams et al., 2012). Evolution relies on individual variation within species, which, intuitively,

we might expect to buffer losses by widening the breadth of conditions under which at least some individuals can survive. Our results are mixed; when competing fig wasps were allowed to evolve high expected net reproduction, evolution led to coexistence more often than when species traits were uniform for all individuals. For lower net reproduction rates, competing species that did not evolve were more likely to result in long-term coexistence. One possible reason for this observation is that species tended to evolve in the direction of increasing fecundity at the cost of dispersal ability. Indeed, although simulations with evolving competitors tended to diverge in fecundities, an overwhelming proportion of these simulations also led to an increase in fecundity values for both species (i.e., both species increased in fecundity, but at different rates such that the difference between them also increased). If the immediate effect of selection pressure is to increase fecundity at the cost of dispersal ability, increased dispersal mortality may lead to evolutionary suicide under the conditions of our model.

The ecological divergence of competitors is an interesting result of our model, suggesting that the storage effect may facilitate ecological character displacement under the conditions described. These results are consistent with two recent models of the storage effect that suggest the evolutionary branching of a population is possible for a broad range of environmental conditions (Abrams et al., 2012; Svardal et al., 2011). For existing communities of competitors that use ephemeral patches, such as those of competing non-pollinator fig wasps, our model predicts trait divergence in local communities for traits that influence both fecundity and dispersal ability.

Spatial storage

For ease of modeling and proof of concept, we model competitive coexistence using only a temporal storage effect. Our model shows that given a minimal set of assumptions, competing non-pollinator fig wasps can maintain positive growth rates and viable population sizes over time. For natural communities of non-pollinating fig wasps, spatial storage

mechanisms and spatial heterogeneity will very likely facilitate competitor coexistence further. In our model, we assume competing wasps move from a single fig with eclosing wasps to another fig with receptive fruit. In nature, multiple figs with eclosing wasps and figs receptive to incoming wasps are likely to overlap temporally, leading to spatial variation for wasps in travel distance to the nearest receptive fig. When such spatial effects are present, the dynamics of populations will be the arithmetic mean of local spatial processes (Hassell et al., 1991; Chesson, 2000). For competing species in non-pollinating fig wasp communities, and ephemeral patch communities in general, such spatial processes should have the effect of lowering the variance of competitive superiority over time because different competing species may be competitively superior in different localities. A lowered variance of competitive superiority will prevent dramatic swings in population sizes, which often lead to extinction in our model. Applying the spatial storage effect model outlined in Chesson (2000) to our fig wasp system indeed suggests that spatial variability should further promote coexistence (A. B. Duthie, *unpublished results*).

Conclusions

Our model shows that long-term coexistence among competing non-pollinator fig wasps is possible when wasps vary in their fecundities and dispersal abilities because of the variability of fig cross-compatibility distances. At times when a receptive fig is near the natal fig of dispersing fig wasps, wasps with high fecundity will have a competitive advantage even if their dispersal ability is poor. When a receptive fig is more distant, wasps that invest to a greater degree in the ability to disperse will have a competitive advantage. We propose this mechanism as a broadly applicable hypothesis for explaining fig wasp diversity. Within non-pollinator communities, a number of other elements of fig ecology will be relevant to understanding wasp coexistence. In addition to dispersal/fecundity trade-offs, some non-pollinating fig wasps vary in resources use (e.g., Kerdelhué et al., 2000) and oviposition timing (e.g., Ranganathan et al., 2010; Ghara

and Borges, 2010), both of which may limit competitive exclusion. Given this diversity of non-pollinator life-histories, and the diversity in non-pollinator community composition among fig species, we emphasize the utility of these communities as a model for the study of competitive coexistence (e.g., Kerdelhué et al., 2000; Hawkins and Compton, 1992) and the evolution of diversity.

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Parameter	Description	Default Value	Source
α	Exp. min. distance to receptive tree (meters)	714.2857	Unpublished data; Figure 1
r_{tar}	Tree volatile radius (meters)	100	–
l_i	Species walk persistence length (meters)	100	–
δ_i	Species emergence rate	0.88	Greeff and Ferguson (1999)
φ	Ovule abundance	10000	Janzen (1979)
τ	Wasp development time	5	Janzen (1979)

Table 1: Default values for modeling competing non-pollinator fig wasps

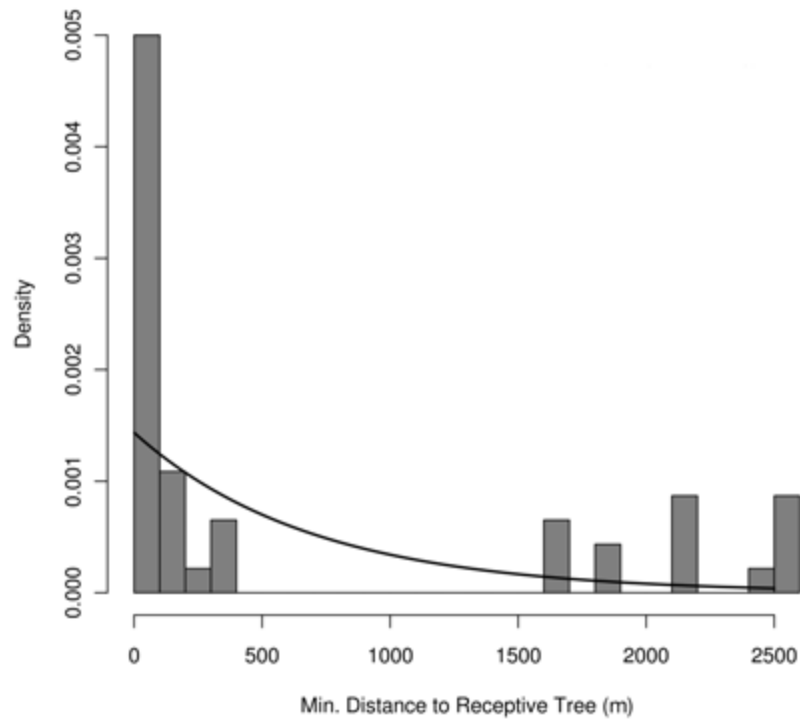


Figure 1: Histogram of distances among *Ficus petiolaris* trees releasing dispersing fig wasps and figs concurrently bearing fruit receptive to wasps. The black line shows the maximum likelihood estimate of the exponential distribution modeling this distance (see text).

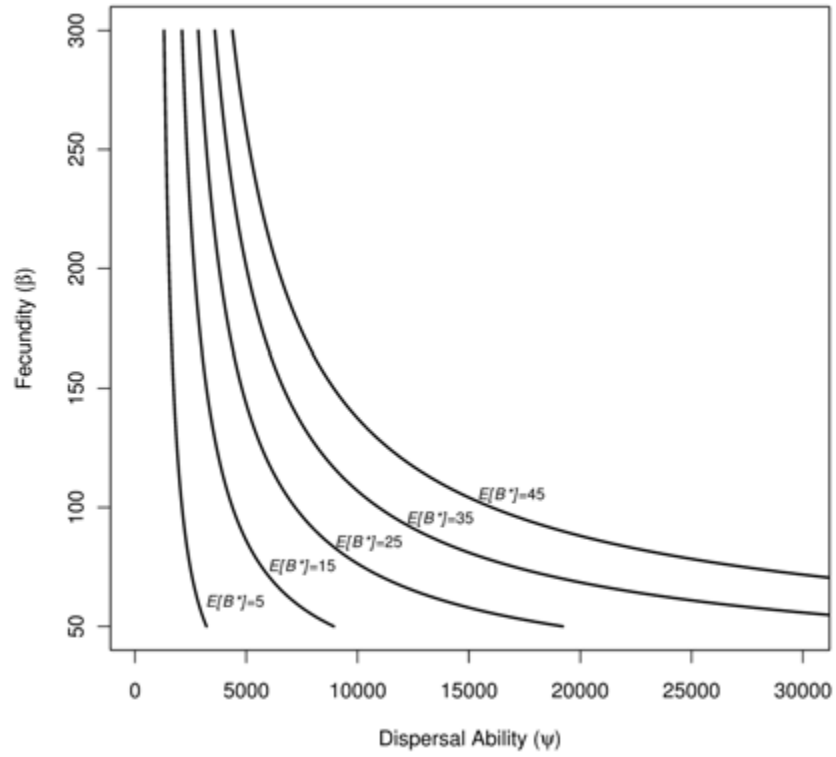


Figure 2: Trade-off lines showing the maximum expected fecundity values allowed in the IBM simulations of nonpollinating fig wasps. Combinations of individual β and ψ that resulted in values above $E[\beta^*]$ lines were not permitted.

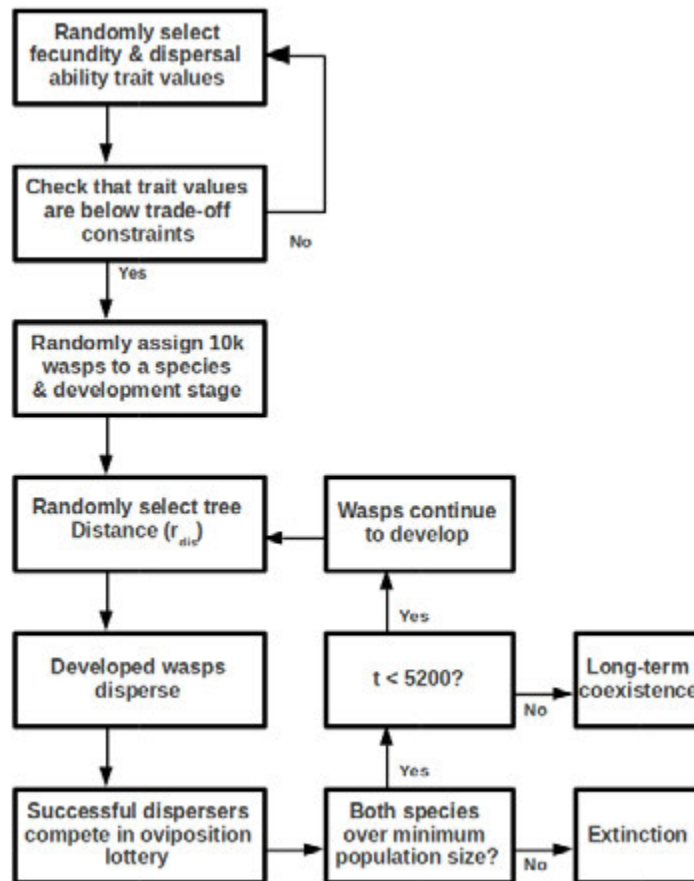


Figure 3: Flow chart of an individual-based model for a single simulation run of competing fig wasps.

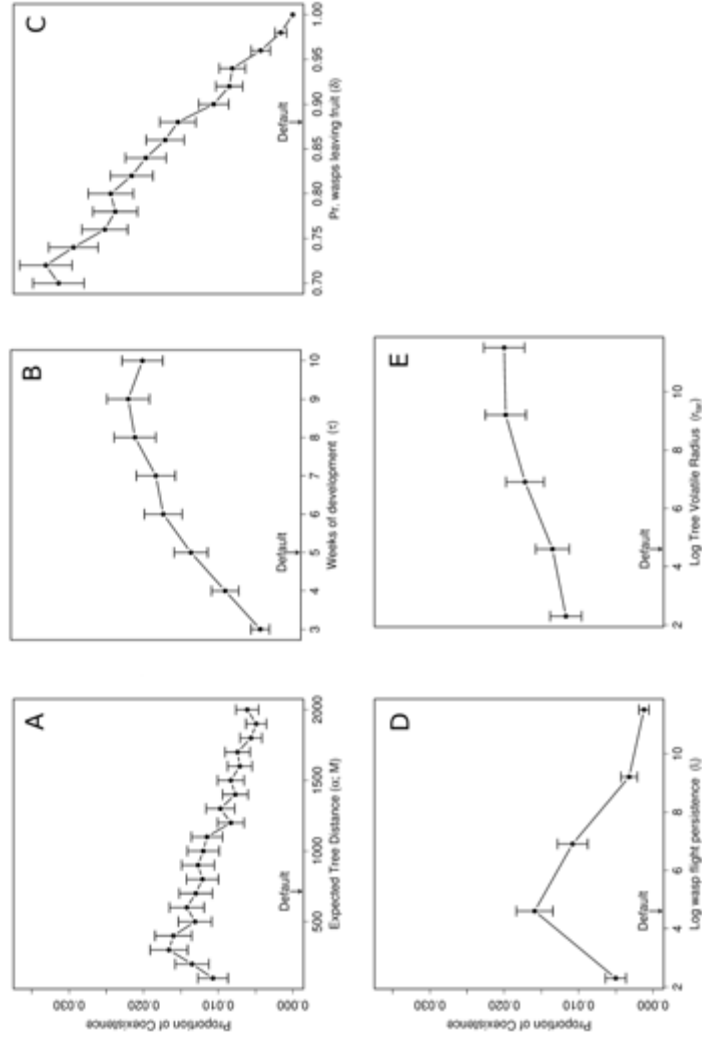


Figure 4: Proportion of simulations in which coexistence criteria were upheld at different expected minimum distances to a receptive fig (A; α), durations of wasp development (B; τ), eclosion rates (C; δ), flight persistence values (D; l_i), and receptive fig volatile radii (E; r_{tar}) for simulated competitor fig wasps. Error bars show 95% confidence intervals.

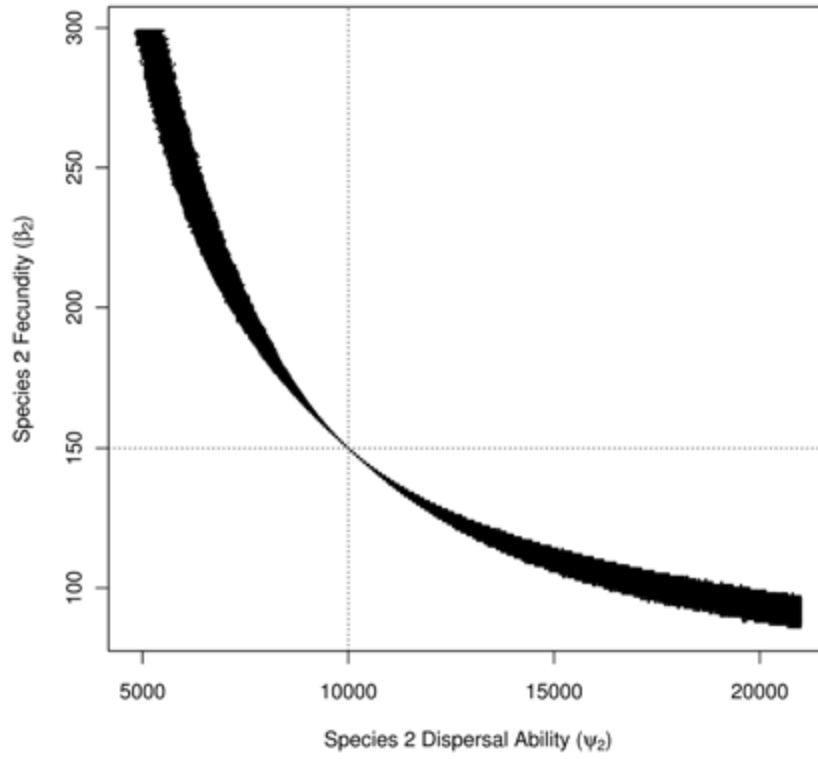


Figure 5: Coexistence along the ranges of β_2 and ψ_2 simulated given $\beta_1 = 150$ and $\psi_1 = 10000$. Solid points represent simulations that resulted in coexistence. The horizontal dotted line shows where $\beta_1 = \beta_2$, and the vertical dotted line shows where $\psi_1 = \psi_2$.

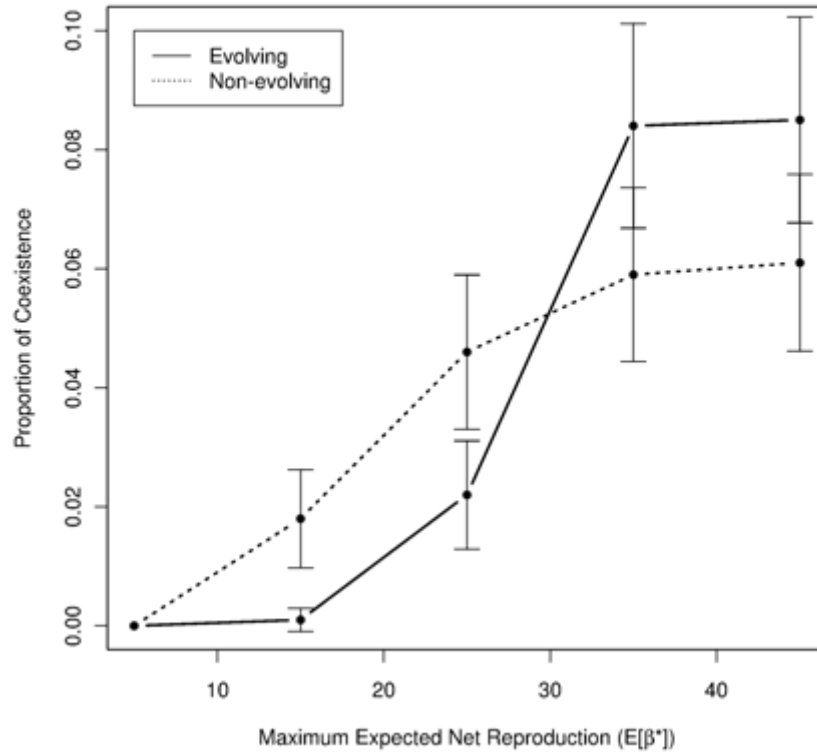


Figure 6: Relationship between the maximum expected net reproductive rate ($E[\beta^*]$) of competing simulated fig wasps and their probability of coexistence. In all simulations, the initial life history values of two competing species are randomly selected and combinations of trade-off values for fecundity (β) and dispersal ability (ψ) are restricted so that wasps cannot increase $E[\beta^*]$ above a maximum value. Simulations in which trade-off values are allowed to evolve are compared to simulations in which trade-off values do not evolve. Error bars show 95% confidence intervals.

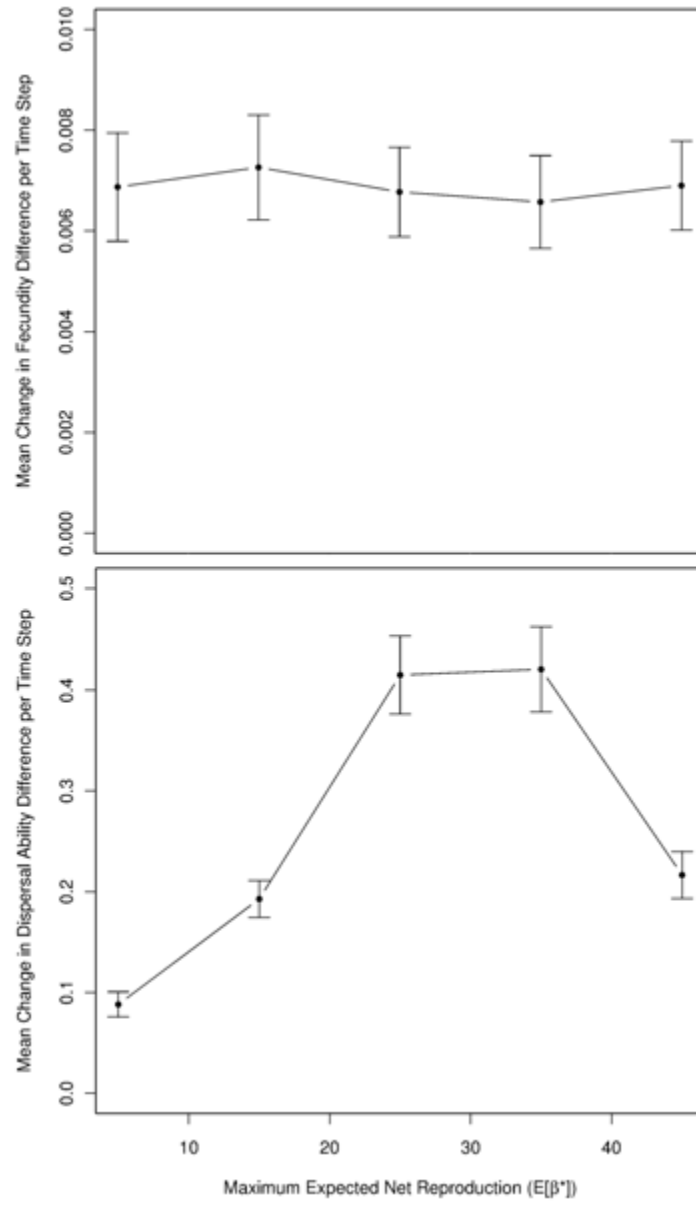


Figure 7: The mean change in species differences in fecundity (top) and dispersal ability (bottom) per time step between two simulated species of fig wasps at different maximum expected net reproductive rates ($E[\beta^*]$). Wasp traits of fecundity and dispersal ability are allowed to evolve in an individual-based model of competitive interactions. Positive values on the y-axis show that the mean difference between species fecundity and dispersal abilities increases, and species are diverging ecologically over a broad range of $E[\beta^*]$. Error bars show 95% confidence intervals.

CHAPTER V. A FLUCTUATING ENVIRONMENT DRIVES COEXISTENCE IN FIVE NON-POLLINATING FIG WASPS

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A manuscript to be submitted to *Science*

Abstract

The ecological principle of competitive exclusion states that species competing for identical resources cannot coexist, but this principle is paradoxical given that ecologically similar competitors are regularly observed. Theory shows coexistence is possible under some conditions if a fluctuating environment changes the competitive dominance of species. We find evidence of an extreme case of such a mechanism in five ecologically similar non-pollinating fig wasps, which migrate long distances from their natal figs to new figs each generation. All five wasp species fall along a common trade-off line between investment in dispersal ability and fecundity, indicating variation in required migration distance among figs to be the driving force for maintaining coexistence. We suggest fluctuating environmental conditions may drive coexistence more generally, especially competitors using ephemeral patches.

Introduction

The coexistence of myriad species of competitors with ecologically similar niches has been a longtime focus of community ecology. Hutchinson (1) observed multiple ecolog-

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ically similar species in a community as paradoxical given the theoretical principle of competitive exclusion, which states that species competing for identical resources cannot coexist (2).

Hutchinson (1) proposed that fluctuating environmental conditions could lead to the coexistence of similar competitors, reasoning that competitive exclusion could be avoided if a fluctuating environment altered the competitive superiority of species rapidly enough for all species to avoid extinction. Subsequent theoretical work has shown Hutchinson's proposal to be supported, but dependent upon the details of particular communities. Whether or not fluctuating environmental conditions can facilitate the long-term coexistence of competitors depends on the covariance between environmental conditions and the effects of competition. If environmental effects on population growth rate are independent of competition, competitive exclusion is expected, with the inferior competitor in the average environment becoming extinct (3). If unfavorable environments are associated with especially strong competition, exclusion is expected to be even more rapid. Long-term coexistence results only when the reduction in population growth caused by an unfavorable environment is associated with weak competition (3; 4). When this occurs, population decline is minimized in unfavorable conditions, serving as a buffer against extinction. Chesson (4) notes that processes of this type can be broadly classified under the general concept of sub-additivity.

Sub-additivity can occur whenever a population contains individuals with different sensitivities to the environment and competition. For example, in many populations, the survival of juvenile individuals may be highly sensitive to the effects of their environment and competition (e.g., seeds and young seedlings), but adult survival may be unaffected by these processes. A subset of the more general concept of sub-additivity is the storage effect (5). Under the storage effect, a subset of individuals in a population are unaffected by environmental variation or competition, incurring a background

rate of mortality that is expected to remain constant over time. The relative growth rates of competing populations are thus influenced solely by the effects of environment and competition on recruitment to the subset of the population that is stored. When recruitment to the storage stage of a population is limited by resource availability and competitors specialize on different environments, sufficient environmental variation results in all competitors having positive long-term (geometric) growth rates when rare, maintaining coexistence (5; 6). The storage effect has been shown to facilitate coexistence among multiple communities of competitors with life histories that include a stage of long term population storage in environments that vary over time (7; 8; 9; 10; 11).

Chesson (12) notes that models including competitors with long-term population storage undergoing temporal changes in competitive dominance promote coexistence with results identical to those of competitors with any length of population storage in which the environment varies spatio-temporally. Spatio-temporal variation occurs when the environment of competitors varies independently over time at all spatial locations. Competitive coexistence incorporating spatio-temporal environmental variation has been modeled in the context of ephemeral patch systems generally (13), with environmental variation among patches interpreted biologically as caused by either variation in patch access or preference, or offspring survival following patch use.

Previously, we have focused on ephemeral patch systems in which resources within patches are discrete (Duthie et al. *In revision*). Using a lottery competition model, we showed that a temporal storage effect can facilitate competitor coexistence given a single functional trade-off between competitor fecundity and dispersal ability when the minimum travel distance to a new receptive patch varies over time. We proposed this mechanism as broadly applicable for competitors using ephemeral patch resources, but focused specifically on the myriad competing species of non-pollinating fig wasps often found using identical resources (fig ovules) in larval development. Here we show that a

single life history trade-off between fecundity and dispersal ability facilitates coexistence in a community of five non-pollinating fig wasp competitors when there is fluctuating variation in travel distance to receptive figs.

The interaction between figs (*Ficus*, Moraceae) and their pollinating wasps (multiple genera, Agaonidae) is a classic example of an obligate mutualism. Figs rely on wasps to disperse pollen (which are usually specific to a fig host), and pollinating wasps complete their development by feeding on a single fig flower as developing larvae; flowers are enclosed within fig fruit (technically and hereafter syconia). The asymmetric costs and benefits for each mutualist, easily quantified by seed and pollinator production, make figs and pollinating fig wasps useful for studying the costs involved in mutualisms (14; 15). And the highly specific nature of figs and their pollinators make fig-fig wasp mutualisms ideal for studying coevolution (16; 17). Typical of most mutualisms (18), figs and their pollinating wasps are exploited by species that receive mutualist resources without paying any costs. These exploiters include multiple species of wasps that feed on developing fig flowers, but do not pollinate. Like pollinators, non-pollinating fig wasps are usually host-fig-specific (19), but unlike the typical one to one pairing between mutualist species, a single species of fig can host between 3 and 30 species of non-pollinators, which are often found within the same fig syconia (20). These species include non-pollinating gallers that feed on fig flowers like pollinators, inquiline wasps that kill pollinators and feed on developing seed tissue (21), and parasitoids that consume other species in larval development. The life histories of species in multiple non-pollinator fig wasp communities have been described in detail (20; 22; 23; 24). Particular attention has been paid to gall-forming species in attempt to assess their impact on fig-fig wasp mutualisms (24; 25; 26). More recently, the high diversity of gallers developing in the flowers of fig species has provoked interest in how gallers in these communities coexist; because multiple species of competitors use a limited resource (fig flowers), competitive exclusion is expected.

Previous studies have called attention to differences in mode (23; 27) and timing (22; 23) of galler oviposition, but it remains unclear how such life history differences could avoid competitive exclusion.

We propose a solution that relies on the ephemeral availability of fig flowers for ovipositing wasps. Syconia development within the crown of individual fig trees is never continuous, and is often synchronous with bouts of reproduction separated by many months and even a few years (28; 29). Under these conditions, fig wasps cannot maintain standing populations on an individual fig tree. Instead, wasps must seek new fig trees with flowers receptive for oviposition. Because most fig species occur at low population densities with highly asynchronous among tree reproductive activity, wasps must routinely disperse long distances, ranging from tens of meters to tens of kilometers (30; 31; 32). Our modeling work shows that the coexistence of multiple competing galler is possible given a wide range of biologically realistic conditions (Duthie et al. *In revision*). Coexistence relies on a change in competitive dominance over time that is dependent on a trade-off in wasp investment in fecundity versus dispersal ability. As the travel distance from a wasp's natal fig to the nearest receptive fig changes over time, so does the optimal investment in fecundity and dispersal ability. When wasp species have a differential investment in these life history characteristics, the competitive dominance of species changes with changing travel distance. Wasps that are developing as larvae in fig syconia are unaffected by this changing travel distance, so their storage serves as a buffer to extinction when distances between natal and receptive fig trees are unfavorable. A critical prediction of this hypothesized coexistence mechanism is an evolutionary trade-off between fig wasp fecundity and the ability of wasps to successfully disperse to receptive figs.

The non-pollinating fig wasp community surrounding *F. petiolaris* (subgenus *Urostigma*) is ideal for testing the predicted trade-off between fecundity and dispersal ability. *F. peti-*

olaris is sparsely-distributed along its range of the Sonoran Desert of Baja California and adjacent mainland Mexico; here we limit our observations to Baja California, where *F. petiolaris* is the only endemic species of fig. *F. petiolaris* is pollinated by a single species of *Pegoscopus* wasp and hosts a diverse and host specific non-pollinating fig wasp community. Five of these non-pollinators gall fig flowers in larval development (Figure 1), ovipositing externally into fig syconia. These galls include three unnamed species of the genus *Idarnes* and two unnamed species of *Heterandrium*. Each species is regularly found within the same fig syconia competing for the same flower resources for larval development. The galler community is large enough to test for a life history trade-off among species, but none of these species is parasitized by other non-pollinators, thus minimizing the potential confounding impact of indirect species interactions. The non-pollinator community also includes a single species of *Aepocerus*, which galls the outer tissue of fig syconia and thus does not compete for access to developing flowers, and its specialist parasitoid of the genus *Physothorax*.

We sampled wasps from five populations spanning a broad geographic range in Baja California. We estimated the fecundities of each of the five galls by determining the egg loads of wasps at the time of eclosion. To assess the ability of galling species to disperse to receptive figs, we used two independent methods. The first of these methods relied on the relative abundances of wasps among fig trees to develop a colonization index (see methods) wherein species with higher colonization index values are relatively better than others at colonizing receptive fig trees. The second method we used was to estimate mean wing loadings for each species of galler; insects with low wing loadings tend to have higher dispersal ability (33; 34). As predicted, we found estimates of fecundity to be negatively correlated with our estimate of colonization index ($P = 0.0038$; $R^2 = 0.9573$; Figure 2a) and positively correlated with wing loading ($P = 0.0261$, $R^2 = 0.8496$; Figure 2b). Qualitative observations also support our predicted life history

trade-off. Within genera, wasp ovipositor length increased monotonically with fecundity and decreased with dispersal ability, suggesting that ovipositor length may inhibit wasp dispersal. All but one species of wasp was found to be pro-ovigenic – having all eggs mature at eclosion (Table 1). Species in which at least some eggs are immature at eclosion are defined as synovigenic, and often have greater longevity than proovigenic wasps (35; 36). In the case of fig wasps, greater longevity is likely to increase the probability of successful dispersal to receptive fig trees. The only synovigenic wasp in our galler community was a species of *Heterandrium*, which also had the highest colonization index and lowest wing loading.

The trade-off between fecundity and dispersal ability observed here strongly supports the hypothesis that fluctuating dispersal distance among fig trees maintains species coexistence in the *F. petiolaris* galler community. We believe that these results can be broadly applied to the understanding of diversity in non-pollinating fig wasp communities, and to communities of ephemeral patch competitors more generally. To our knowledge, this is the first empirical evidence supporting the hypothesis that the storage effect facilitates coexistence among ephemeral patch competitors. A storage effect is necessary to explain diversity in this community because long term coexistence of species is impossible without population storage due to the extinction risk in periods of prolonged unfavorable conditions (when dispersal distance to receptive figs is suboptimal).

Understanding the mechanisms that maintain coexisting species is a central goal of ecology and of critical importance to species conservation. The galler community of non-pollinating fig wasps associated with *F. petiolaris* is an extreme example of how a fluctuating environment can maintain an entire suite of competitors. In this community, a single fluctuating environmental variable and life history trade-off is the driving force for coexistence among five species of competitors. This study shows that a fluctuating environment can play a major role in structuring competitor communities, and that

galling fig wasp communities are an excellent model system for studying how the storage effect maintains coexistence in competitors on ephemeral patch resources.

Methods

Data collection

We sampled the galling community from 451 syconia of 17 *F. petiolaris* trees distributed across five sites located from far southern to north-central Baja California. All samples were collected in 2010. We sampled nearly mature fig syconia, wherein all species of fig wasp are mature, but have yet to leave syconia. For each syconia collected, a count of foundress pollinator corpses was recorded to assess the number of successfully arriving pollinator wasps (range: 0-4). After collection, syconia were partially cut open and placed in individual vials overnight (min 12 hrs) to allow wasps to emerge. Emerged wasps were preserved in 95% ethanol and shipped to Iowa State University where counts of all species were obtained for each fruit. We observed positive counts for all species of gallers in one or more syconia in which no foundresses arrived.

Estimating fecundity

To estimate fecundity, we followed the procedure of Ghara and Borges (22) used to estimate egg loads in *F. racemosa*. We dissected wasps in a phosphate buffer saline solution and under a stereomicroscope. An acetocarmine stain was used to facilitate the counting of mature and immature oocytes. Mature and immature oocytes were counted under a compound microscope to estimate species fecundities.

Estimating wing loadings

Normally, wing loading is calculated as the ratio of body mass to wing area. Because fig wasp mass is difficult to estimate with precision, we used body volume instead (37; 38). Body volume (V) of wasps was calculated by summing estimates of wasp head, thorax,

abdomen, and ovipositor volume. To estimate head volume, head width (W_h) and height (H_h) were measured. We assumed a spherical head shape and estimated head radius as $r_h = (\frac{1}{2})(\frac{W_h}{2} + (\frac{H_h}{2}))$; using this estimate of head radius, we estimated head volume using the formula to determine the volume of a sphere, $V_h = (\frac{4}{3})\pi(r_h^3)$. To estimate thorax volume, we measured thorax length (L_t) and width (W_t), then used the formula describing the volume of an ellipsoid, $V_t = (\frac{4}{3})\pi(L_t)(W_t)^2$. We estimated abdomen volumes in the same way as we did thorax volumes. To estimate ovipositor volumes, we measured ovipositor length (L_o) and width (W_o), then used the formula describing the volume of a cylinder, $V_o = \pi(L_o)((\frac{1}{2})(W_o))^2$.

To estimate wing surface area, either the left or right forewing and hindwing were removed for each wasp, and images of both wings were taken using a stereoscope camera. We used ImageJ software to estimate wing surface area in the collected images, then multiplied this estimation by two to estimate total wing surface area.

Developing and estimating colonization index

We developed a colonization index to estimate the relative abilities of each galler species to successfully disperse to receptive fig trees. To construct this index, we first estimated the mean density of developing wasps (pollinators and non-pollinators) in the syconia of the fig tree crops to estimate how difficult each crop was to colonize when it was receptive. The logic for our method assumes the total density of eclosing wasps in a crop will increase if the crop was easy for wasps to colonize when receptive. A similar technique is well-known and widely-used in estimating spatial heterogeneity in parasitism risk (39), and is acknowledged to be advantageous in encompassing risk factors that are difficult to measure or unknown (40). Ease of wasp colonization among crops of receptive syconia may vary with crop spatial or temporal proximity to trees with eclosing wasps, but potentially also due to unmeasured or unknown environmental variables that influence crop efficacy in attracting fig wasps. For this reason, we use eclosing wasp

density per syconia volume as an estimate of the relative ease of crop colonization at the time of receptivity.

To determine the relative ability of each galler to colonize receptive crops, we estimate the sensitivity of each species' abundance to crop colonization difficulty. For any galler species, the number of eclosing wasps in a crop is expected to increase as a function of the number of successfully colonizing conspecifics arriving to oviposit. The abundance of eclosing wasps of a species that is relatively adept at colonization will not decrease dramatically with crop colonization difficulty, but the abundance of a species that is a poor colonizer will drop much more quickly for harder to colonize crops (in an extreme case, if a species had no hindrance to crop colonization, wasp arrival would be unaffected by, and eclosing wasp abundance would not decrease at all with, colonization ease. In contrast, if a species was inept at colonization, it would be entirely absent from crops with even a modest difficulty of colonization). For 17 crops, we regressed ease of crop colonization against per syconia galler density; relatively high slope values indicate that species density is especially sensitive to ease of crop colonization. Slopes were negated so that higher values reflected relatively higher species colonization abilities, which were used as values for our colonization index. Because males of *Idarnes* species have not been classified, only female wasps were used in constructing the colonization index.

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Label	Genus	OI	Wing (mm^2)	Wing (mm)	Vol. (mm^3)	Ovi. (mm)
LO1	<i>Idarnes</i>	1.0	2.108 \pm 0.086	1.75 \pm 0.04	2.50 \pm 0.25	5.52 \pm 0.09
SO1	<i>Idarnes</i>	1.0	1.575 \pm 0.050	1.48 \pm 0.03	1.63 \pm 0.11	3.03 \pm 0.06
SO2	<i>Idarnes</i>	1.0	1.651 \pm 0.062	1.51 \pm 0.03	1.60 \pm 0.13	2.84 \pm 0.04
Het1	<i>Heterandrium</i>	0.56 \pm 0.04	2.814 \pm 0.143	1.95 \pm 0.04	2.37 \pm 0.20	0.34 \pm 0.01
Het2	<i>Heterandrium</i>	1.0	2.022 \pm 0.066	1.69 \pm 0.03	2.27 \pm 0.14	0.65 \pm 0.01

Table 1: Gallling fig wasps associated with *Ficus petiolaris* (all species unnamed). Ovigeny index (OI) is calculated by dividing the number of mature wasp eggs by the total number of eggs upon wasp eclosion. Total wing area (Wing [mm^2]) includes two forewings and two hindwings for each species. Wing length (Wing [mm]) describes forewing only. Volume (Vol.) measures total body volume. Ovipositor length (Ovi.) measures the external sheath of each species. All \pm values indicate standard errors.

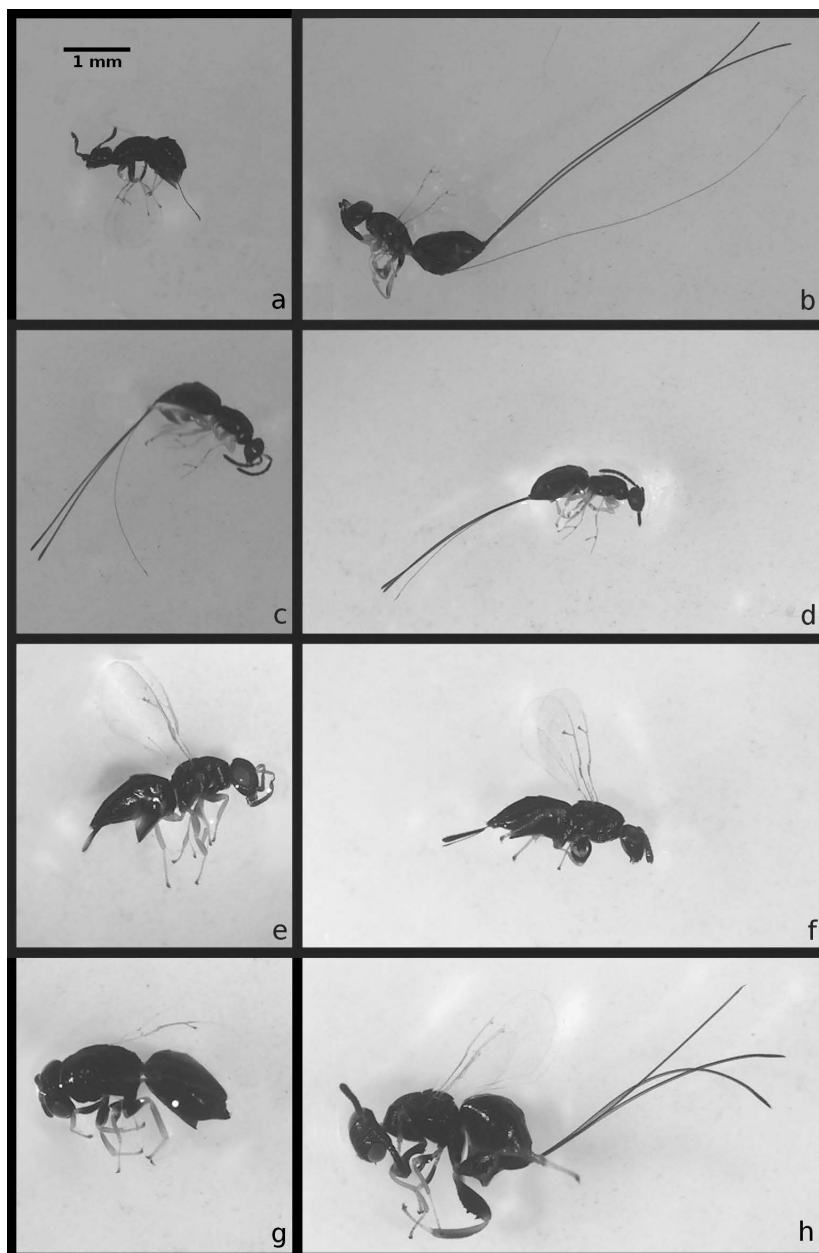


Figure 1: Community of fig wasps associated with *F. petiolaris*, which is pollinated by a wasp of the genus *Pegoscapus* (a). Five galls shown include three species of *Idarnes* (b-d) and two species of *Heterandrium* (e-f). Additionally, a species of *Aepocerus* (g) feeds on an inner layer of *F. petiolaris* syconia and is parasitized by a species of *Physothorax* (h). All wasps pictured developed from the same fig syconia from an *F. petiolaris* in Baja California.

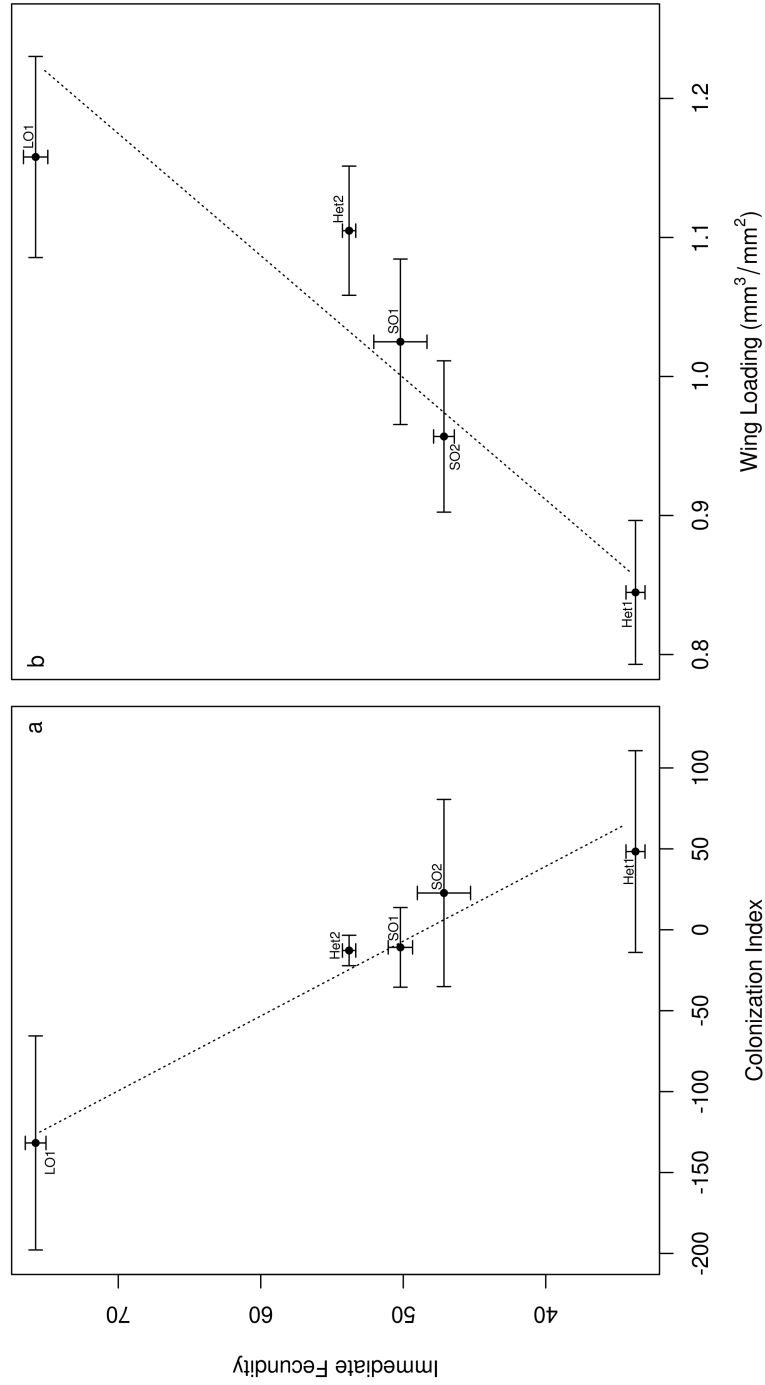


Figure 2: Correlation between wasp immediate fecundity and colonization index (a), and wasp immediate fecundity and wing loading (b) in the non-pollinating galler community associated with *F. petiolaris*. Immediate fecundity is defined as the mature egg load upon wasp eclosion. Galling wasps include one long ovipositor species of *Idarnes* (LO1), two short ovipositor species of *Idarnes* (SO1 SO2), and two species of *Heterandrium* (Het1 Het2). Error bars show standard errors around the means.

CHAPTER VI. GENERAL CONCLUSIONS

This dissertation demonstrates the importance of spatial, temporal, and spatio-temporal mechanisms in influencing species interactions within ephemeral patch systems. This work extends prior theory using individual-based modeling to show that the autocorrelation of habitat can have a strong influence on plant-pollinator communities. Pollinators in plant-pollinator communities must regularly disperse to receptive plants, and in model systems often feed on ephemerally available seeds. Because the probability of a seed being eaten by a pollinator will be directly affected by the number of pollinators that visit a plant flower, the frequency at which seed-eating pollinators visit flowers has a major impact on the costs and benefits associated with the mutualism. High pollinator visitation increases per capita pollination, but also the number of seeds consumed. The number of pollinators visiting a plant is expected to increase with local plant density. Where plant habitat is especially dense, local plant density will be high. If pollinator dispersal is limited, plants in these regions of high density will support high densities of pollinators that are able to move efficiently between plants. As a result of frequent pollinator visitation, plants with many nearby conspecific neighbors will produce disproportionately more pollinators than seeds. Because pollinators compete with non-pollinating exploiters of mutualisms, plants in these locations will also have lowered rates of exploitation. This is the case for the plant-pollinator interaction between the Sonoran Desert rock fig (*Ficus petiolaris*) and its wasp pollinator (*Pegoscapus*), wherein fig trees with a higher number of conspecific neighboring trees are visited by more foundress pollinators, produce fewer seeds, and are less likely to be exploited by non-pollinators. Because the costs, benefits,

and stability of mutualisms with seed-eating pollinators are all strongly influenced by pollinator and exploiter birth rates, and because figs in particular are often a keystone resource for local frugivores, the work in this dissertation is of broad interest to ecology, evolution, and conservation.

This dissertation also extends prior theory on competitors in ephemeral patch systems through the introduction of lottery models, which are used demonstrate how a temporal storage effect facilitates competitor coexistence when competitors develop within patches in overlapping generations. Conceptually unique to this work, the mechanism generating the temporal environmental variance on which coexistence relies is space itself, in the form of varying minimum between patch dispersal distance. When the minimum dispersal distance required to move from ephemeral patch to ephemeral patch changes over time, the superiority of competitors using patch resources can also change over time if they invest differently in fecundity versus dispersal ability. Given a trade-off in fecundity and dispersal ability, coexistence is predicted over a wide range of biologically realistic parameters for non-pollinating competitor fig wasps. An empirical prediction of this modeling work is that the fecundities of competitors in fig wasp communities will be negatively correlated with wasp dispersal abilities. Egg load estimates and two independent metrics of wasp dispersal ability show that non-pollinating gallers associated with *F. petiolaris* have negatively correlated fecundities and dispersal abilities. These results demonstrate that wasp population storage and a fecundity-dispersal ability trade-off are critical mechanisms for maintaining fig wasp diversity in at least one fig wasp community, and likely many others. And they more broadly demonstrate the importance of a fluctuating environment on species interactions and coexistence in ephemeral patch communities.